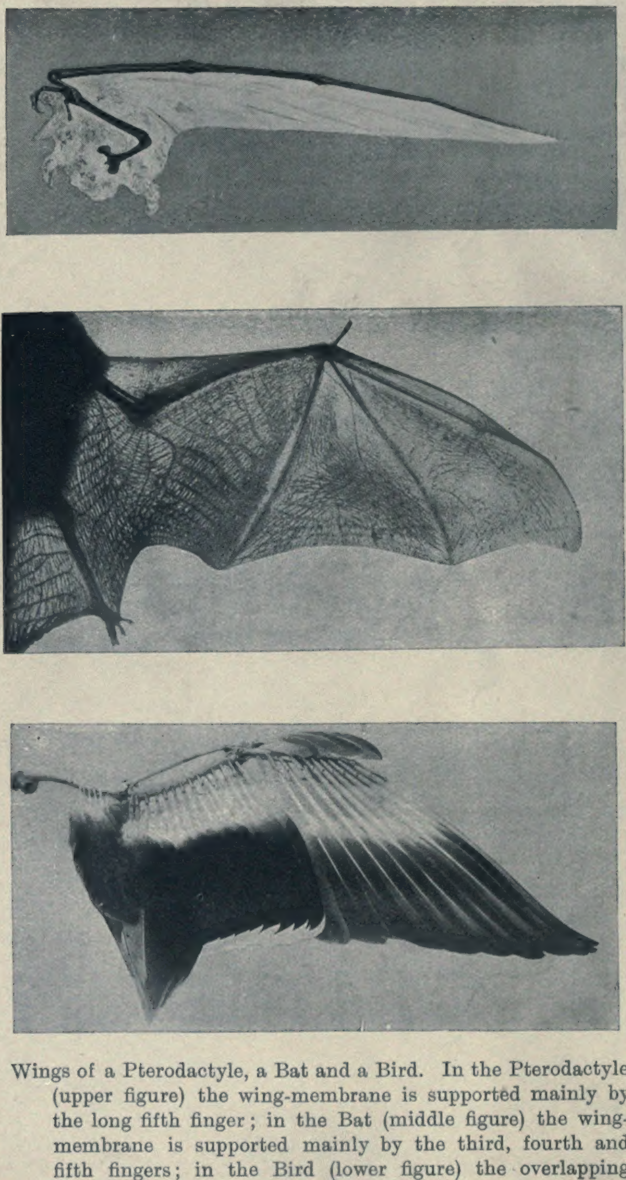

Wings of a Pterodactyle, a Bat and a Bird. In the Pterodactyle (upper figure) the wing-membrane is supported mainly by the long fifth finger; in the Bat (middle figure) the wing-membrane is supported mainly by the third, fourth and fifth fingers; in the Bird (lower figure) the overlapping feathers form an almost impervious layer for beating the air (see 85).

From Sir E. R. Lankester's *Extinct Animals*, 1905, p. 233.

BRITISH MUSEUM (NATURAL HISTORY)

SPECIAL GUIDE No. 6.

GUIDE TO THE EXHIBITION OF SPECIMENS ILLUSTRATING THE MODIFICATION OF THE STRUCTURE OF ANIMALS IN RELATION TO

FLIGHT

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PREFACE.

At the present time, when such rapid advances are being made in the efficiency of aeroplanes and the control of navigable balloons, and when so much attention is being given by inventors to the construction of machinery adapted to the requirements of aviation, it becomes a matter of particular interest to consider the various modifications of structure by which animals have attained command of the air; and the present exhibition, comprising 166 mounted objects and 12 microscopic specimens, has been arranged for the purpose of elucidating the subject in a popular manner.

In the series of specimens exhibited the adaptation of each kind of flying animal for aerial locomotion is explained, and the changes that must have taken place in the structure of the body before the animal could really fly are indicated; and attention is drawn to the remarkable fact that the power of flight has been evolved independently in different groups of animals—Bats, Birds, Pterodactyles and Insects.

In all the human attempts at aviation that have met with any degree of success the part of the apparatus that sustains the weight in the air (planes or gas-bag, as the case may be) is distinct from the driving apparatus (propeller and its engine); but a study of the specimens here displayed shows that in flying animals the energy is generated by the contraction of muscles directly connected with the wings, and that the latter, by a regular beating or flapping action, both support the body in the air and force the body through it.

Among the exhibited specimens are preparations illustrating the mechanical principles involved in the linkage and leverage of the skeletal parts, dissections and models explaining the action of the power-producing apparatus (elevator and depressor muscles) and its relation to the skeletal parts, prepared specimens showing

the structure and shape of the flight membranes, and specimens explaining the mode of folding of the wings when at rest.

The exhibition is not limited to animals that can truly fly, but includes also examples of animals which move through the air by scudding, gliding or parachuting, without expending energy from the time when they leap off to the time when they alight, such as the so-called Flying Squirrels, Flying Phalangers, etc.

The selection and preparation of the specimens for exhibition, and the writing of this Guide-book are the work of Dr. W. G. Ridewood.

For the frontispiece the Trustees of the British Museum are indebted to Messrs. A. Constable and Co., Ltd.; of the 44 text-figures, 26 have been specially drawn, and most of the remainder have appeared in guide-books previously published by the Trustees; for figs. 5 and 8 acknowledgment is due to Messrs. A. and C. Black, and for figs. 15 and 17 to Messrs. Macmillan and Co., Ltd.

L. FLETCHER,
Director.

British Museum, Natural History.
July, 1913.

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MODIFICATION OF THE STRUCTURE

OF

ANIMALS

IN RELATION TO

FLIGHT.

INTRODUCTION.

The cases containing the specimens illustrating the structure of flying animals are all situated on the East* side of the Central Hall, in the Bay or Recess marked VII.†

The series exhibited includes various kinds of animals which agree in possessing some capacity for moving through the air. Of these animals, some are capable of true flight, propelling themselves through the air by a flapping of wings, *e.g.* Birds, Bats, Pterodactyles ‡ and Insects. Others are enabled by some form of outspread membrane or fold of skin to break their fall when leaping from a branch, and by adopting an oblique attitude in their descent to scud for considerable distances through the air, *e.g.* Flying Lemurs, Flying Squirrels, Flying Phalangers, Flying Lizards, Flying Snakes, etc.

The independent modification of parts of the body for the purpose of aerial locomotion in the different groups of animals is of considerable interest in the light of the theory of "evolution." The wings of the Bird, Bat and Pterodactyle (see frontispiece) are

* The entrance of the Museum is at the *South* end of the Central Hall, and the main staircase is at the *North* end; the side of the Hall to the right of the visitor on entering is the *East*.

† The Bays or Recesses around the Central Hall are denoted by numerals. On the East side, the Bay nearest the Huxley statue is No. X, and that by the side of the main staircase is No. VI.

‡ The Pterodactyles being extinct, the evidence of their capacity for flight is necessarily indirect, and the conclusion presumptive.

instances of homoplasy, or convergence, being structures evolved independently as organs of true flight in three separate divisions of the Vertebrate phylum, Birds, Mammals and Reptiles; and they are not to be explained as wings inherited as functional organs of flight from the ancestral stock from which all Birds, Bats and Pterodactyles have originated. This is shown by the fact that, although in these three groups of Vertebrates it is the pectoral limb that has been transformed into a wing; yet the transformation has been effected differently in the three cases. In all three groups the fundamental type of limb skeleton is the same, and such bones as the humerus, radius, ulna, carpal bones, metacarpal bones and phalanges can be clearly and readily identified (see 85).* Yet in the Bats the skin-fold is stretched between the arm bones and the greatly elongated bones of the second, third, fourth and fifth fingers, and extends along the body to include the hind leg and tail; in the Pterodactyles the skin-fold is supported by the bones of the arm and leg and the great fifth finger, the second, third and fourth fingers being free; in the Birds the resistance to the air is afforded, not by a fold of skin, but by a layer of feathers, which are attached at their basal ends to the bones of the arm and hand.

The wings of Insects are again different. They are not transformed limbs as are the foregoing, but are expansions of the outer case or exo-skeleton, and project sideways from the back of the animal. Further than this, the wings are in typical instances two pairs in number, although in many cases, *e.g.* Moths, Wasps and Water-Bugs, there are special locking devices by which the two wings of the same side act together as one sheet.

In all these cases (Birds, Bats, Pterodactyles and Insects) the wings are hinged at their bases, and provided with powerful muscles, so that they can be raised and depressed, and thus made to beat the air and maintain the body in, and propel it through the air.

In the gliding Mammals, the so-called Flying Lemurs (*Galeopterus*), Anomalures (*Anomalurus*, *Idiurus*), Flying Squirrels (*Petaurista*, *Sciuropterus*, etc.) and Flying Phalangers (*Petaurus*, etc.), there is presented another instance of homoplasy, the fold of skin by which the animal is enabled to scud or glide downward

* The specimens exhibited bear distinctive numbers printed in large figures. The numerals quoted in brackets in this guide-book refer to the specimens bearing those numbers, and the numerals printed in heavy type at the beginning of the paragraphs in the body of the guide-book have the same significance.

through the air being a new development in each of the separate groups of Mammals, and not a structure possessed by the common ancestors of these groups. Indeed, there is a probability that even within the group Marsupialia the patagium or skin-fold has been independently evolved in the three Australian genera *Petaurus*, *Petauroides* and *Acrobates*, for these are not closely related Phalangers.

In the cases just mentioned the skin-fold or patagium is held in position during the act of gliding by the outstretched arms and legs, and in some cases the tail, but in the Flying Lizard (*Draco*) the arms, legs and tail are free, and the fold of skin at the side of the body is supported by certain of the ribs which are greatly elongated for the purpose.

The question of flight in the Flying Fishes is a vexed one. There can be no doubt, from the records of careful observers, that the greatly expanded pectoral fins of *Exocoetus* are agitated as the fish moves through the air, but it would appear that any flapping of the fins as wings that does occur is of less importance than the service rendered by the fins in checking the descent of the fish into the water again (see 44–46).

It is of interest to note that the only animals that fly are either Vertebrates or Insects. The so-called Flying Copepods (see 100), minute oceanic Crustaceans, merely spring out of the water and fall back again, and thus have less claim to be regarded as flying animals than even the Flying Squirrels and Flying Lizards. The Parachute Spider of Australia, *Attus volans* (97), also, cannot be regarded as a flying animal. It is a very small jumping Spider with little flaps at the sides of the abdomen which enable it to take longer leaps than other Spiders of the same size.

CASE I.

MAMMALS.

Bats.

1-2. A Bat (Fox-Bat or Flying Fox, *Pteropus giganteus*) mounted in the attitude of flight, and a skeleton of the same species with the bones arranged as they would be disposed in the flying animal.

Bats are the only Mammals possessing the power of true flight; the Flying Lemurs, Flying Squirrels and Flying Phalangers

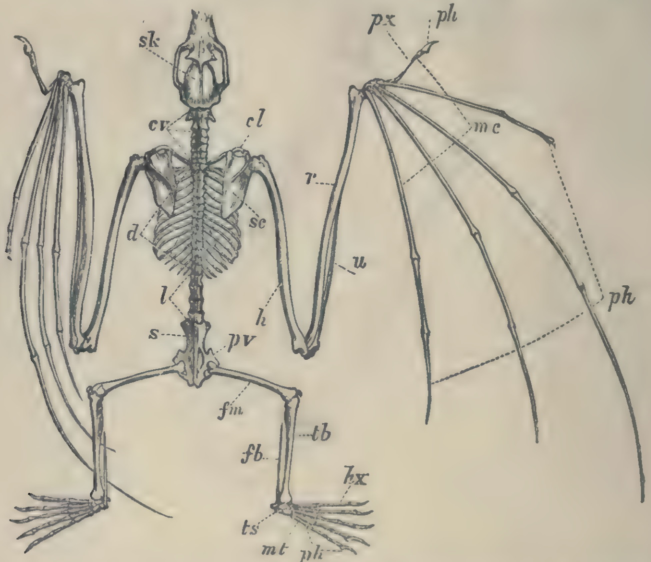

Fig. 1.—Skeleton of a Bat (Fox Bat or Flying-Fox, *Pteropus giganteus*), showing the elongation of the bones of the arm and hand for the support of the large wing-membrane (see 2). *cl*, clavicle; *cv*, cervical vertebrae; *d*, dorsal vertebrae; *fb*, fibula; *fm*, femur; *h*, humerus; *hx*, great toe, or hallux; *l*, lumbar vertebrae; *mc*, metacarpals; *mt*, metatarsals; *ph*, phalanges; *pv*, pelvis; *px*, thumb, or pollex; *r*, radius; *s*, sacral vertebrae; *sc*, scapula; *sk*, skull; *tb*, tibia; *ts*, tarsus; *u*, ulna.

are able to scud down through the air, but they cannot beat the air and rise in it to a higher level.

The wing-membrane of Bats is a double fold of skin (see 5),*

* See footnote on page 2.

which extends outward from the side of the body and hind legs, and encloses and is supported by the bones of the arm, fore-arm and hand. The thumb is mostly free and has a claw (frontispiece, middle figure), the second digit is in insect-eating Bats set close to the third without any considerable extent of membrane between; the greatest expanse of membrane is between the side of the body and the fifth, fourth and third fingers. In some Bats (insect-eating Bats in particular) there is also a membrane between the legs, supported in the middle by the tail, but this membrane does not share in the flapping of the wings. In fruit-eating Bats the tail is mostly short, and the interfemoral membrane is reduced or wanting.

With few exceptions Bats are nocturnal in habit; the eyes are in many cases reduced, and the external ears are frequently of great size, and in some Bats there are large leaf-like expansions of sensitive skin around the nostrils which enable the animals to steer a clear course between trees and rocks, and to recognise and pursue the insects on which they feed.

In size Bats vary from the small animals found in this country to the great edible Bat (*Pteropus vampyrus*) of Java, which measures five feet across the fully extended wings.

In the skeleton the chief points to be noticed are the elongation of the bones of the third, fourth and fifth digits, the elongation of the radius and the slenderness of the ulna (fig. 1). The keel of the sternum is seen in side view in specimen 6 (fig. 2).

3. A Bat, *Pteropus giganteus*, showing the mode of folding of the wings when at rest. The right wing is shown partially closed, the left completely closed.

When settling, the Bat hangs head downward by its toes from the branch of a tree or the edge of a rock, the curved claws pointing towards the front of the animal, owing to a curious rotation which the leg bones have experienced.

In the closing of the wing the angle between the arm and the fore-arm becomes reduced until the latter lies alongside the former. At the same time the bones of the hand approach one another until they become nearly parallel to the fore-arm, so that the whole of the wing is brought up close to the side of the body. The closed wing then wraps over the chest and abdomen, and protects these parts during the period of rest.

4. *Taphozous nudiventris*, a Bat of the family Emballonuridae. In most Bats the middle or third digit of the wing can in a state of repose be bent more or less towards the ventral surface, but in

the Bats of the family Emballonuridae the phalangeal portion of the third finger bends back on the dorsal surface of the wing, and to such an extent that the first phalangeal bone comes to lie parallel with the metacarpal bone.

5. Right wing of a Bat (*Pteropus vampyrus*) with the membrane between the ulnar bone and the fifth digit partially split to show that it is composed of two separable layers of skin. Compare with this the preparation of the Moth's wing, 101.

6. Portion of skeleton of a Bat (*Pteropus vampyrus*), left side, showing the extent of the keel of the sternum for the attachment of the depressor muscles of the wings (fig. 2).

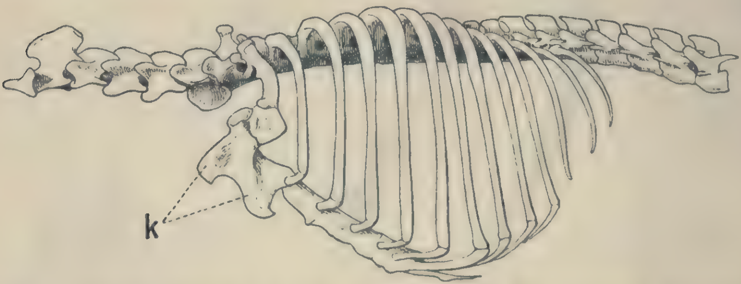

Fig. 2.—Thoracic skeleton of a large Fruit Bat (*Pteropus vampyrus*), together with the cervical and lumbar vertebrae, seen from the left side. k, the keel of the sternum, to which the depressor muscles of the wings are attached (see 6).

7–8. Dissection of the shoulder of a Bat (Fruit Bat, *Pteropus vampyrus*) and explanatory sketch (see fig. 3). In Bats the principal muscles concerned in elevating and depressing the wing during flight are the *deltoideus* and the *pectoralis major*. The *deltoideus* (shown in blue in the explanatory sketch) on contraction raises the wing; it is inserted into the upper * part of the first bone of the wing (humerus), and takes its origin from the upper surface of the shoulder blade (scapula) and from a high-standing process of it (the acromion). The scapula itself is not a rigid part of the skeleton, but is held in position by the contraction of the *trapezius* and other muscles. The *pectoralis major* (shown in red in the explanatory sketch) is the largest muscle in the body of the Bat, and by its contraction brings about the depression of the wing during flight. It arises mainly from the side of the

* I.e. dorsal in the extended wing.

sternum, but partly from the clavicular bone. It is inserted into the anterior and under surface of the basal end of the humerus, which bone is freely hinged with the scapula. The drawing forward of the extended wing is effected mainly by the clavicular

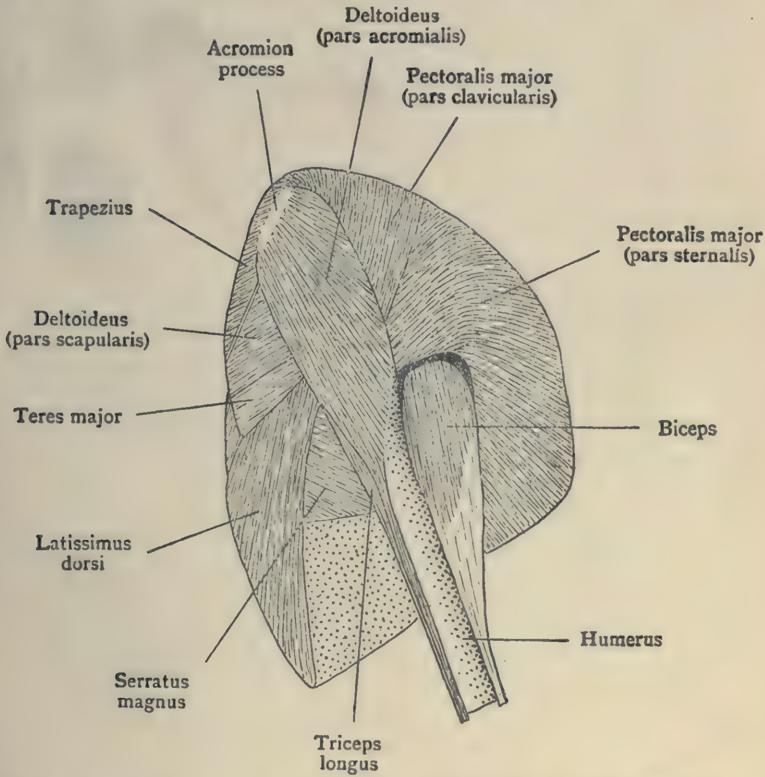

Fig. 3.—Dissection of the shoulder of a Bat (Fruit Bat, *Pteropus vampyrus*), showing the principal muscles that move the wings during flight (see dissection 7).

part of the *pectoralis major*, with which is intimately associated a clavicular part of the *deltoideus*, not shown in the dissection; the drawing back of the wing is brought about chiefly by the *teres major* and the *latissimus dorsi*.

9. Simple model to illustrate the mechanical principles involved in the elevating and depressing of the wing of a Bat. The brass lever, representing the wing, is hinged upon a brass

frame, the upper, plate-like piece of which stands for the scapular bone, and is held in position by white cords (*trapezius* and other muscles), while the lower, rod-like piece stands for the clavicular bone, and is rigidly fixed at its inner end against a piece of board which occupies the position of the middle plane of the body. The brass lever is actuated by two cords. The upper one (blue), standing for the deltoid muscle, is attached to the upper surface of the brass plate; the lower one (red), standing for the great pectoral muscle, is attached to the board at a part which may be considered as the equivalent of the keel of the sternum. Both of these cords are tied to the lever at points more remote from the middle plane of the body than the fulcrum or centre of rotation. If the blue cord be tightened and the red cord slackened the lever rises; if the red cord be tightened and the blue cord slackened the lever is pulled down. The tightening and slackening of the cords find their equivalents in the Bat in the contraction (shortening) and relaxation (release from shortening) of the muscles.

10. Photograph of Indian Fruit Bats (*Pteropus giganteus*) in flight.

Flying Lemurs.

11. Flying Lemur, *Galeopterus volans* (fig. 4). The species of *Galeopterus* (*Galeopithecus*) constitute the group of Mammals called Dermoptera, and although called Flying Lemurs, are allied to the Insectivora rather than to the Lemurs. They subsist, however, mainly upon vegetable food. A patagium or extension of the skin at the sides of the body between the fore and hind legs, and extending forward to the neck and backward to the tail, and even between the fingers and toes, forms a kind of parachute, which enables the animal to float or glide through the air from tree to tree. The animals cannot fly, nor rise in the air; their movements in the air are always those of descent. The Flying Lemurs occur in the Malay Archipelago; they are nocturnal in habits, and in the daytime hang head downward from the trees. Flying Lemurs are sometimes called Taguans, but this term has also been applied to the Flying Squirrels and the Flying Phalangers.

Rodents.

12–14. Asiatic Flying Squirrels, *Sciuropterus nigripes*, from the Philippine Islands, *Petaurista nitida rajah*, from Borneo, and

Petaurista leucogenys, from Japan. The species of *Petaurista*,* *Sciuropterus* and allied genera are arboreal Rodents of the family Sciuridae, occurring mostly in the Oriental region, although species are found in North America, Eastern Europe and Siberia. They have a skin-fold or patagium extending along the side of the body between the fore and hind limbs, and continued feebly along the neck, and in *Petaurista* for a short distance along the base of the tail. In *Sciuropterus* the flank membrane is relatively narrower than in *Petaurista*, and the tail is flatter. In some

Fig. 4.—Flying Lemur (*Galeopterus volans*), showing the fold of skin along the side of the body which enables the animal to glide through the air (see 11).

species of *Petaurista* (14) the tail is bushy. The Flying Squirrels cannot fly, but the patagium enables them to leap greater distances than ordinary Squirrels. They at first descend in a long swoop, sometimes as much as 60 or 70 yards, and rise slightly just before reaching the bough upon which they intend to alight. Flying Squirrels are nocturnal in habit, and spend the day in hollow trees, where they generally associate in colonies.

* Formerly *Pteromys.*

15. Tail of *Sciuropterus sagitta.* The tail is flattened, and somewhat resembles the flat bristly tail of the small Anomalure *Idiurus macrotis*, 17.

16–17. African Flying Squirrels, or Anomalures, *Anomalurus fraseri* and *Idiurus macrotis*, from the Cameroons. The species of *Anomalurus* (fig. 5), *Idiurus* and allied genera are arboreal

Fig. 5.—An African Flying Squirrel (*Anomalurus fulgens*), showing the fold of skin along the side of the body which enables the animal to glide through the air (see 16).

From *Study of Mammals*, by Flower and Lydekker, 1891, p. 449; after Alston, *Proc. Zool. Soc.*, 1875.

Rodents of the family Anomaluridae, occurring mostly in West and Central Africa. They present a strong superficial resemblance to the true Flying Squirrels, although their relationship to the Sciuridae is rather remote. They have a skin-fold or patagium extending along the side of the body between the fore and hind limbs, feebly developed in front of the fore limb and behind the hind limb, and not extending along the tail. The animals cannot fly, but the patagium enables them to glide or scud down obliquely

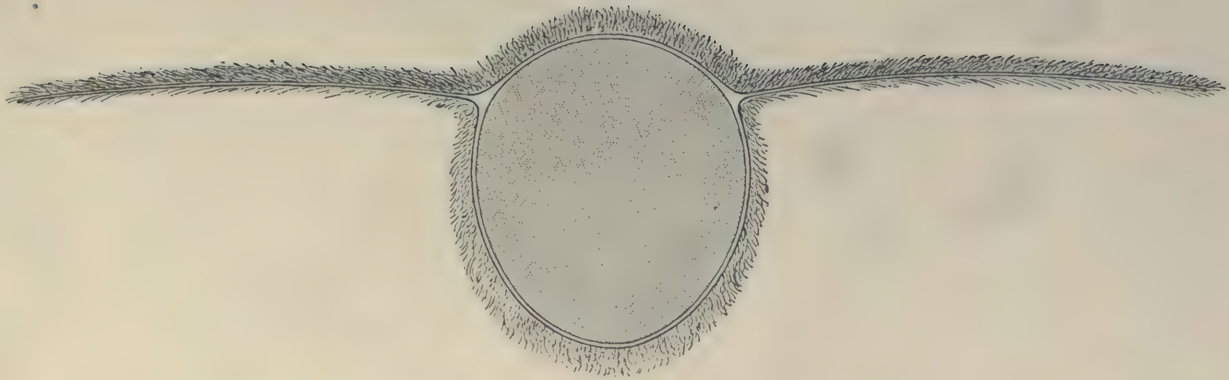

Fig. 6.—Section across the body of an African Flying Squirrel (*Anomalurus beecrofti*), about mid-way between the fore and hind limbs, showing that the patagial membrane consists of skin only—two layers of skin, with thick fur above and scanty hairs below. The drawing is about two-thirds of the natural size (see 18).

for long distances from one branch to another. The under surface of the root of the tail has a double row of spiny scales which assist the animal in climbing trees. Anomalures are sometimes termed Scaly-tailed Flying Squirrels.

18. Middle portion of the body of an African Flying Squirrel (*Anomalurus beecrofti*), seen from behind (fig. 6). The patagial membrane arises fairly high up the side of the body, and consists of skin only—two layers of skin, with thick fur above and scanty hairs below.

19. Skeleton of an African Flying Squirrel, *Anomalurus erythrogaster*, showing that the patagial fold of skin between the fore and hind limbs has no skeletal support other than the rod of cartilage (C) which projects from the elbow.

20–21. Skeleton of the right fore limb of an African Flying Squirrel, *Anomalurus beecrofti*, and of an Asiatic Flying Squirrel,

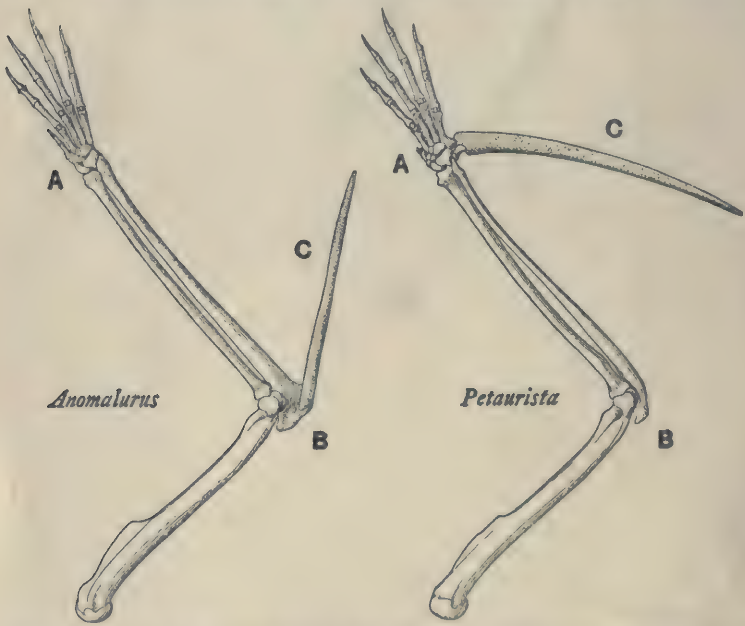

Fig. 7.—Skeleton of the fore limb of an African Flying Squirrel (*Anomalurus beecrofti*) and an Asiatic Flying Squirrel (*Petaurista magnificus*). In the former the cartilaginous rod that stiffens the front part of the patagial membrane arises from the elbow; in the latter it arises from the outer edge of the wrist. A, wrist; B, elbow; C, rod of cartilage (see 20–21).

Petaurista magnificus, showing the rod of cartilage which stiffens the patagial membrane. Of interest, as tending to show that in the African Flying Squirrels and the Asiatic Flying Squirrels the lateral patagial membrane has been independently evolved, is the fact that the membrane in the former is supported by a rod of cartilage that projects outward from the elbow, while in the latter the support is afforded by a rod of cartilage projecting from the wrist (fig. 7). Such rods of cartilage do not occur in the skeletons of ordinary Squirrels.

MARSUPIALS.

22–24. Flying Phalangers, *Petaurus breviceps*, *Petauroides volans* and *Acrobates pygmaeus*. The Flying Phalangers of Australia are species of unrelated genera of Marsupials, *Petaurus*

Fig. 8.—A Flying Phalanger (*Petaurus sciureus*), showing the fold of skin along the side of the body which enables the animal to glide through the air (see 22).

From *Study of Mammals*, by Flower and Lydekker, 1891, p. 154.

(fig. 8), *Petauroides* and *Acrobates*, with soft silky fur and a skin-fold or patagium extending along the side of the body between the fore and hind limbs, and feebly developed along the front edge of the fore limb. These Phalangers cannot fly, but the patagium enables them when leaping from a high branch to glide or float obliquely down to a lower branch of some distant tree.

25. A young Flying Phalanger, *Petaurus breviceps*, showing that the patagial membrane is relatively less developed in the young than in the adult. Compare with the adult, 22.

26. Skeleton of a Flying Phalanger, *Petaurus australis*, showing that there are no skeletal supports for the patagial membrane other than the limb bones (contrast with 20–21).

REPTILES.

Pterodactyles.

Pterodactyles (Ornithosauria or Pterosauria) are extinct winged Reptiles, which lived in the Secondary or Mesozoic Period, and the remains of which are found in England, Germany, Kansas, etc. The wings are large (figs. 9 and 10), and the support of the wing-membrane is afforded by the bones of the arm, the greatly enlarged fifth finger,* and the leg. The digits of the hand, other than the fifth, are slender, and the hind foot has four feeble digits furnished with claws, and in some cases a fifth toe is present in addition. The tail is long in some, and short in others. There is a slight keel to the sternum, far less prominent than in flying Birds. In size the Pterodactyles range from small animals no larger than Sparrows to others with a wing span of 18 feet.

27. Drawing of the restored skeleton of *Pteranodon*, a great Pterodactyle from the Cretaceous of Kansas, etc. (fig. 9). The span across the wings is about 18 feet. The skull is prolonged into a sharp toothless beak, and the hinder part of the skull is produced into a bony spine. The tail is extremely short. A restored skeleton of *Pteranodon* is exhibited in the Geological Department of the Museum, and a restored model is shown over the doorway leading from the Reptile Gallery towards the Shell Gallery in the Zoological Department.

* That the great wing-finger is the fifth is the generally accepted view, but Williston (*Journ. Geol.*, *Chicago*, xix, 1911, p. 696) is disposed to revert to Cuvier's interpretation of the digit as the fourth.

28. Restoration (natural size) of the sternum of *Pteranodon*, a great Pterodactyle from the Cretaceous of Kansas, etc. The lateral edges of the sternum have articulations for four or five pairs of ribs. The hinder part of the sternum is an extremely thin plate of bone; the front part, or manubrium, is massive, and on its upper surface has two articular facets for the large coracoid bones. Unlike flying Birds the Pterodactyles have but a slight keel to the sternum for the attachment of the muscles of flight.

29. Cast of the anterior portion of the sternum of *Ornithochirus*, a great Pterodactyle from the Cambridge Greensand of Cambridge, etc. The specimen is seen from the left side.

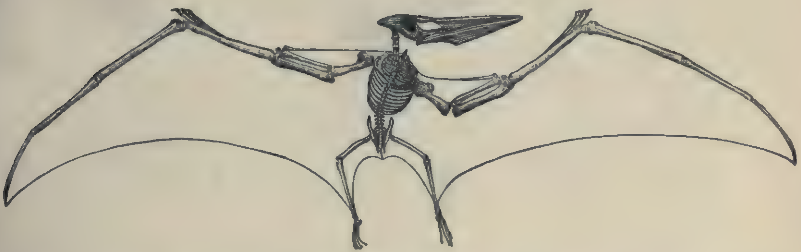

Fig. 9.—Skeleton of a very large Pterodactyle, or Flying Reptile (*Pteranodon occidentalis*), from the Cretaceous of Kansas. The span across the wings is about 18 feet.

30. *Pteranodon* sp., notarium or mass of fused anterior thoracic vertebrae, ventral view; from the Upper Cretaceous of Kansas. Compare 31, fig. 4.

31. Four figures of the notarium (fused mass of anterior thoracic vertebrae) of *Pteranodon* sp. Fig. 1, left side view; fig. 2, oblique view; fig. 3, dorsal view; fig. 4, ventral view. (From G. F. Eaton, "Osteology of *Pteranodon*," Mem. Connecticut Acad., Arts and Sciences, vol. ii, 1910, pl. viii.)

While in all but certain aquatic Vertebrates (Fishes, Whales, Sirenians) and some Snakes (Python, Boa) the upper bones (ilia) of the pelvic girdle are regularly connected with a fused mass of vertebrae (the sacrum)*, a connection between the upper bones (scapulae) of the pectoral girdle and a fused mass of vertebrae (the notarium) is very unusual. It occurs in the Pterodactyles and in Skate-like Fishes.

* In most Frogs the sacrum consists of one vertebra only.

Figs. 1 and 2 show the lateral depression in the upper ridge of bone into which the upper extremity of the scapula fits.

32. Ulnar bone of a large Pterodactyle, *Ornithochirus* sp., from the Lower Chalk of Snodland, Kent. In Pterodactyles, as in Birds, many of the bones are pneumatic; they are very thin in texture, and the interior was occupied in life by air-sacs in communication with the lungs. In the specimen here shown the thinness of the bone is apparent in the fractured parts.

33. Restored model, one-fourth (linear) of the natural size, of *Dimorphodon macronyx*, from the Lower Lias of Lyme Regis. In *Dimorphodon* the head is large, the tail is long, and the fifth digit of the hind limb and the tail assist the fore limb in supporting the wing-membrane.

34. Drawing of a long-tailed Pterodactyle, *Rhamphorhynchus muensteri*, natural size; copied from the figure of a nearly complete skeleton from the Lithographic Stone (Kimmeridgian) of Eichstädt, Bavaria, published by O. C. Marsh (American Journal of Science, series 3, xxiii, 1882, pl. 3). The outlines of the wing-membrane are well defined. The long slender tail ends in a leaf-like expansion which clearly served as a steering apparatus. A cast of this specimen is shown in the Geological Department of the Museum.

35. Drawing of *Rhamphorhynchus muensteri* (fig. 10) as restored by O. C. Marsh (l.c. p. 256).

Fig. 10.—Restoration of a Long-Tailed Flying Reptile (*Rhamphorhynchus muensteri*), from the Upper Jurassic (Lithographic Stone) of Eichstädt, Bavaria. One-seventh natural size.

After O. C. Marsh.

36. Cast of the wing of *Rhamphorhynchus gemmingi*, a Pterodactyle from the Lithographic Stone (Kimmeridgian) of Eichstädt, Bavaria. The extent of the wing-membrane is particularly well defined (see frontispiece, upper figure). The specimen of which this is a cast is in the Palaeontological Museum at Munich.

37. Drawing of a small, short-tailed Pterodactyle, *Pterodactylus spectabilis*, natural size; copied from the figure of a complete skeleton from the Lithographic Stone (Kimmeridgian) of Eichstädt, Bavaria, published by H. von Meyer (Palaeontographica, vol. x, 1861, pl. 1). A cast of the specimen is shown in the Geological Department of the Museum.

LIZARDS.

38–39. Flying Lizard or Flying Dragon, *Draco spilopterus*. In the various species of *Draco* (e.g. *Draco*

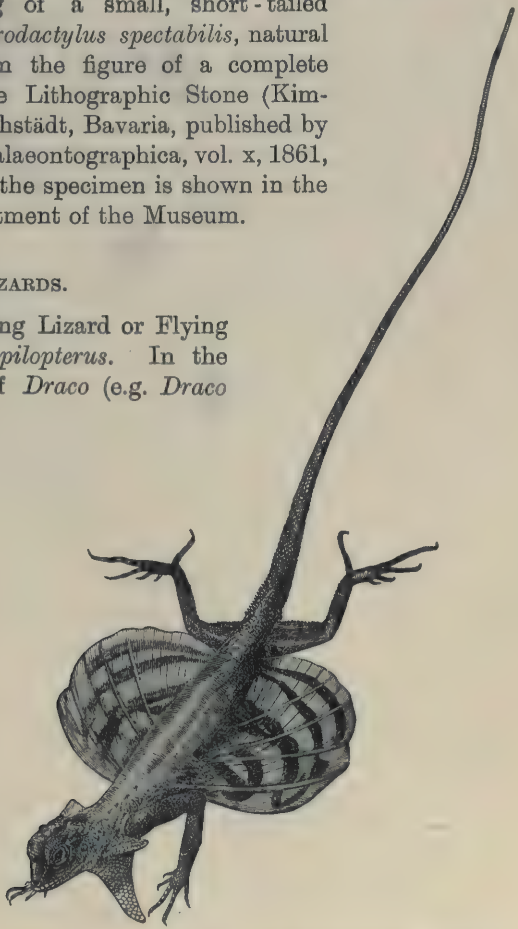

Fig. 11.—A Flying Lizard, or Flying Dragon (*Draco taeniopterus*), showing the fold of skin along the side of the body which enables the animal to glide through the air (see 38).

spilopterus, *D. taeniopterus* (fig. 11), *D. volans*) the skin at the sides of the body is extended to form a patagium, supported by

some of the ribs, which are greatly elongated. The fore and hind limbs remain free. By means of the patagium the Lizards can glide obliquely downward from bough to bough; they cannot fly. In a state of rest the ribs are sloped backward so as to lie up against the sides of the body, and the patagium is thus closed. The species of *Draco* occur mostly in the Malay Peninsula and Archipelago, and the average length is between eight and ten inches. Specimen 38 shows the form of the body with the ribs and membrane fully spread; 39 shows the appearance of the animal when crawling.

40. Skeleton of Flying Lizard, *Draco spilopterus*, showing the remarkable length of the ribs that serve to support the lateral patagial membrane.

41. Flying Gecko (so-called) or Fringed Gecko, *Ptychozoon homalocephalum*. The Fringed Gecko of the Malay countries has lateral expansions of the skin along the sides of the neck, body, tail and limbs, and between the toes, which, it has been suggested, may possibly be used by the animal for breaking its fall when it leaps from bough to bough. In certain other Geckos, however, such as the Bark Geckos, there are similar expansions of skin, but more rough and irregular, and these and the peculiar colour markings on the head and back render the animal difficult to detect as it clings close up against the bark of a tree. The fringes of *Ptychozoon* may perhaps be in like manner cryptic in function (see N. Annandale, *Ann. Mag. Nat. Hist.* (7), xv, 85, 1905, p. 31).

Snakes.

42. A Flying Snake of Borneo, *Chrysopelea chrysochlora*, in the attitude of descending through the air. Certain arboreal snakes of Borneo, namely, *Chrysopelea ornata*, *Chrysopelea chrysochlora*, and *Dendrophis pictus*, when descending from a height, launch themselves into the air obliquely downward, keeping the body rigid and perfectly straight. On such occasions the transverse section of the body is not circular in outline, but is concave on the under side, owing to a drawing in of the ventral scales by a special muscular contraction (see R. Shelford, *Proc. Zool. Soc.* 1906, pp. 227–230).

AMPHIBIANS.

43. A Flying Frog of Borneo, *Rhacophorus nigropalmatus*, with the fingers and toes spread to display the extensive membrane or web (fig. 12). The various species of so-called

Fig. 12.—Flying Frog (*Rhacophorus nigropalmatus*), with the toes spread to show the membrane, or web, which is present in both fore and hind feet (see 43).

Flying Frog (*Rhacophorus*), although arboreal in habit, and provided with adhesive discs at the extremities of the fingers and toes, are more nearly allied to the Common Frogs (*Rana*) than to the Tree-Frogs (*Hyla*). The fore and hind feet are so broadly webbed in the species exhibited that they have been believed by

some to serve as "planes," enabling the animal to take long flying leaps from branch to branch. The genus *Rhacophorus* is distributed through India and Ceylon, Madagascar, East Indies, China and Japan; the most widely known species are those of Borneo.

FISHES.

44–46. Flying-fish, *Exocoetus.* The various species of Flying-fish (*Exocoetus volitans*, *E. spilopterus* (fig. 13), etc.) are

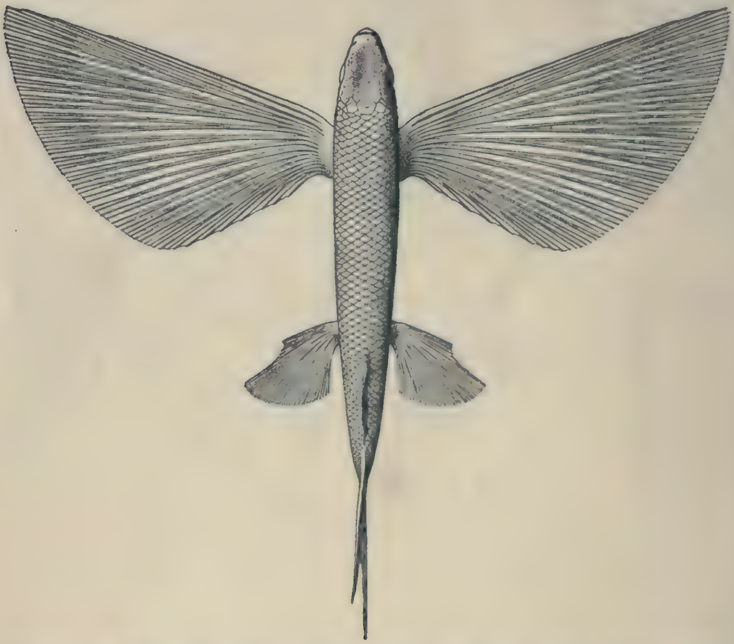

Fig. 13.—A Flying-fish (*Exocoetus spilopterus*), seen from above (see 44–46).

allied to the Skippers and Garfish. They live in shoals in tropical and sub-tropical seas, and are pursued by large fishes such as the Tunny and Albacore.

The question whether Flying-fishes really fly, whether, that is to say, their pectoral fins are moved as organs of flight like the wings of Birds and Bats, is a subject of much contention. Careful observers have recorded the fact that when moving through the

air the fins are agitated, and this may be readily admitted; but while some claim that the fins are flapped like the wings of a Bird, with the definite object of beating the air and propelling the body as well as maintaining it in the air, others regard the rapid movements of the large pectoral fins as like the flapping of a flag waved rapidly through the air.

Two or three hundred yards is no uncommon flight, and although the fishes may rise sufficiently high out of the water to find themselves stranded upon the deck of an ocean-going steamship, Flying-fishes cannot maintain themselves in the air for any considerable period of time, and the probability is that the enlarged fins serve to maintain the body in the air rather than to propel it through the air. The muscles at the base of the pectoral fin are not enlarged in the same proportion as the fin itself, as would be the case if the fins were used as true wings; they are nevertheless considerably larger than the corresponding muscles of allied fishes which have not the pectoral fins enlarged. The initial impetus is provided by the great muscles of the tail; the fishes leave the water with great velocity by a powerful movement of the tail, and move through the air at a rapid rate until they reach the water again, when another lashing movement of the tail may start them afresh through the air without the whole of the body entering the water. The fact that a Flying-fish can change the direction of its course in the air points to the movement being something more than a mere scudding or gliding action.*

The largest species (e.g. *E. californicus*) are about eighteen inches in length. In some species the pelvic fins are enlarged, and evidently assist the pectorals during the movement of the fish through the air; in all species the lower lobe of the tail fin is longer than the upper, a feature clearly correlated with the facility with which the fish darts out of the water.

47. Flying Gurnard, *Dactylopterus volitans* (fig. 14). The various species of *Dactylopterus*, known as Flying Gurnards, have

* For a discussion of the question whether Flying-fishes fly, see:— K. Möbius, *Zeitschr. f. wiss. Zool.* xxx. Suppl. 1878, pp. 343–382; C. O. Whitman, *Amer. Naturalist*, xiv, 1880, pp. 641–653; A. Seitz, *Zool. Jahrb., Abth. Syst.* v, 1890, pp. 361–372; F. Dahl, *Zool. Jahrb., Abth. Syst.* v, 1890, pp. 679–688; F. Ahlborn, *Zool. Jahrb., Abth. Syst.* ix, 1896, pp. 329–338; G. E. H. Barrett-Hamilton, *Ann. Mag. Nat. Hist.* Apr. 1903, pp. 389–393; C. D. Durnford, *Ann. Mag. Nat. Hist.* Jan. 1906, pp. 158–167, and Nov. 1906, pp. 327, 328; P. Rendall, Zoologist, Jan. 1912, p. 39; and other papers cited by these authors.

the pectoral fins divided into two parts, the hinder of which is greatly expanded in the adult, and enables the fish to move through the air like the Flying-fish (*Exocoetus*), though for shorter

Fig. 14.—Flying Gurnard (*Dactylopterus volitans*) (see 47).
From Günther's *Study of Fishes*, 1880, p. 481.

Fig. 15.—An African Fresh-water Flying-fish (*Pantodon buchholzi*) (see 48).
From Boulenger, *Camb. Nat. Hist.* vii, p. 559.

distances.* The Flying Gurnards inhabit tropical and warm seas; the best known is *Dactylopterus volitans*, of the Mediterranean Sea and temperate and tropical parts of the Atlantic Ocean. The largest species are about eighteen inches in length and twenty-four inches in width when fully spread.

* See H. N. Moseley, A Naturalist on the "Challenger," 1879, p. 571.

48. African Fresh-water Flying-fish, *Pantodon buchholzi* (fig. 15). *Pantodon* is a brightly coloured little fish of the Congo and Niger Rivers, which leaps out of the water, and flutters through the air for some little distance before falling back into the river. Of interest in this connection is the fact that the first Congo specimen caught by a European was captured above the water by means of a butterfly net. *Pantodon* is one of the lower Teleostean fishes, belonging to a special family, the Pantodontidae, allied apparently to the Osteoglossidae. The length of the fish is about three or four inches.

49–50. American Fresh-water Flying-fish, *Gastropelecus*. Several species of *Gastropelecus* occur in the rivers of British Guiana, and are remarkable for the manner in which they dart out of the water into the air. The fishes are small and laterally

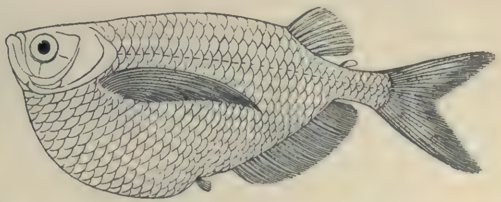

Fig. 16.—A South-American Flying-fish (*Gastropelecus sternicla*) (see 50).

compressed, and with long and curved, but not particularly large pectoral fins. They dart forward for a distance of forty feet or more, beating the water with their pectoral fins, the upper part of the body alone being exposed, and the sharp keel of the breast acting as a cut-water. They then leave the water entirely for a distance of five or ten feet, and when exhausted fall sideways into the water again.* These fishes belong to the group of the Characinid fishes, which includes the Cariba and Dorado of South America, and the Tiger-fish and Moon-fish of Africa. Two species are shown, *Gastropelecus strigatus* and *G. sternicla* (fig. 16).

51. *Pegasus volitans*, a little fish found on the sandy shoals of the coasts of Japan, China, India and Australia. The pectoral fins are broad and horizontal, like wings, but so far as locomotion in the air is concerned, the fishes can hardly do more than skim

* See C. H. Eigenmann, Freshwater Fishes of British Guiana, Memoirs of the Carnegie Museum, v, Pittsburgh, 1912, p. 47.

a short distance above the surface of the water.* The dried bodies of these fishes are frequently used by the Chinese, in conjunction with beetles, shells and bits of coral, in the ornamentation of fancy boxes, many of which are brought to England by sailors and travellers as curiosities.

52. Remains of an extinct Flying-fish, *Chirothrix lewisi.* The species of *Chirothrix* (fig. 17) are extinct Teleostean fishes, the remains of which are found in the Upper Cretaceous strata of Mount Lebanon. Their affinities are doubtful, but they are probably

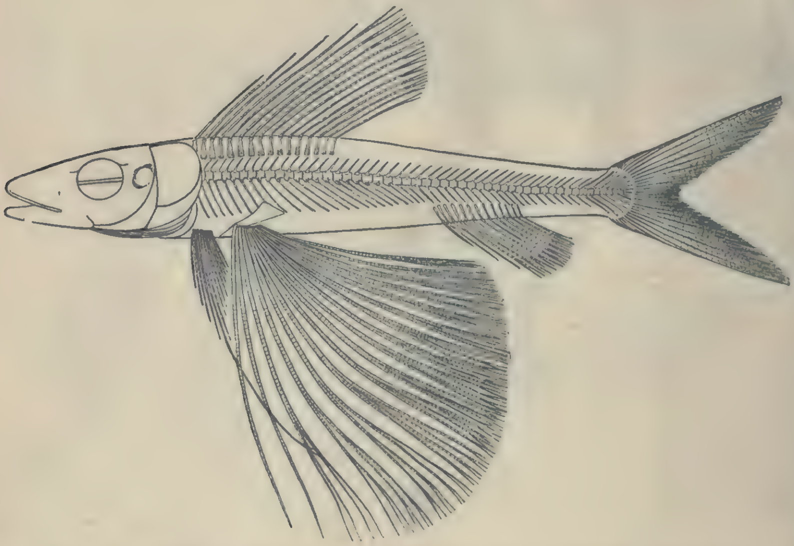

Fig. 17.—Restored Skeleton of a Fossil Flying-fish (*Chirothrix libanicus*), from the Upper Cretaceous of Mount Lebanon (see 52, 53). (× ⅘.)

From *Camb. Nat. Hist.* vii, p. 615; after A. Smith Woodward, *Cat. Foss. Fishes*, iv, 1901, p. 281.

related to the Scopelidae. The pelvic fins are of such great size that it has been suggested that the fish employed them for moving through the air, and that it was therefore as much a "Flying Fish" as are *Exocoetus* and *Dactylopterus* at the present day. The determination of the large fins as pelvic rather than pectoral is based upon the structure of the limb-girdles, those parts of the internal skeleton with which the fin-rays articulate. The length

* See F. Day, Fishes of India, 1875–78, p. 280.

of the fish is about five inches. Several other extinct fishes have been described as Flying-fish, e.g. *Thoracopterus* and *Gigantopterus* of the Upper Trias of Lower Austria, *Dollopterus* from the Upper Muschelkalk of Jena, and *Exocoetoides* from the Upper Cretaceous of Mount Lebanon.

53. Sketch of restored skeleton of *Chirothrix libanicus.* (Copied from "Cat. Foss. Fishes, Brit. Mus.," iv, 1901, p. 281.)

CASE 2.

BIRDS.

54–55. A Mallard or Wild Duck (*Anas boscas*) mounted in the attitude of flight, and a skeleton of the same species of Bird with the bones arranged as they would be disposed in the flying animal.

In Birds the sheet or layer that beats the air is composed mainly of large feathers, the remiges, which project outward and backward from the fore-arm and hand, and overlap one another in such a manner as to present an almost unbroken layer. The gaps between the quills of these large wing-feathers are closed by smaller feathers, called the wing-coverts (see 56), which also invest the fleshy part of the wing. Along the front edge of the wing there stretches a double fold of skin, the patagial membrane; it extends across the angle between the humerus and the radius, and its free edge is strengthened by a strong elastic cord.

Birds vary greatly in size; some of the Humming Birds rank among the smallest, whereas the largest Birds capable of flight are the Albatros and Condor. The Ostrich is larger than these, and the extinct Moa of New Zealand and the *Aepyornis* of Madagascar were flightless birds of still greater size.

Although the power of flight is very general in Birds, it is by no means universal in the class, several species of different groups having wings too small and weak to raise the body from the ground. In addition to the Ostrich, Moa and *Aepyornis* just mentioned, and the other Ratite Birds—Rhea, Cassowary, Emu and Apteryx—the Dodos (extinct), Penguins, some Auks and Rails, a species of Cormorant and a Parrot, have lost the power of flight. In Penguins, although the wing is useless as an organ of flight, it forms a most efficient paddle for locomotion in the water.

In the skeleton of Birds the chief points to be noticed are the absence of the fourth and fifth digits of the fore limb, and the reduction of the other three digits, there being as a rule only one phalanx in the thumb, and only two and one respectively in the second and third digits. The metacarpal bones of the second and third digits are united at their proximal and at their distal ends (see 79, Gannet). The sternum is provided with a keel of variable dimensions (see 82), this keel being a median plate of bone for the attachment of the great pectoral muscles, which by their contraction cause the beating

Fig. 18.—Right Wing of a Bird, showing the disposition of the feathers (see 56). 1, primary remiges; 2, secondary remiges; 3, major coverts of primaries; 4, major coverts of secondaries; 5, median coverts; 6, minor coverts; 7, marginal coverts; 8, remiges of bastard wing; 9, scapulars.

of the wing. The vertebral column of the tail is shortened up (except in the extinct Bird *Archaeopteryx*, 86), the hindermost vertebrae being fused into a single bone, the pygostyle, to which the large tail-feathers, the rectrices, are attached (see 92–96).

56. Left Wing of a Bird (Mallard or Wild Duck, *Anas boscas*), upper view. In the wing of a Bird the resistance to the air is afforded, not by a continuous membrane as in Bats, Pterodactyles and Insects, but by a series of overlapping feathers, which on the down-beat of the wing are forced together to form an impervious sheet.

Of the large flight feathers of the wing (remiges), those attached

to the bones of the hand are termed "primaries," and those between the wrist and elbow joints are called "secondaries" (fig. 18). The primaries vary in number from nine to twelve, the secondaries from six (Humming-birds and Swifts) to thirty-seven (Albatros).

The basal parts of these flight feathers and the front part of the wing are covered, on both upper and under surfaces, by smaller feathers, "coverts" or "tectrices," disposed in several series, as explained in the preparation here shown. The major coverts are important, in that they close the spaces between the quills of the flight feathers, and thus render the wing as a whole one continuous sheet for resisting air-pressure.

In the autumn Birds usually moult, i.e. shed their feathers, and develop a new set. Birds thus have an advantage over Bats, in that any injury to the feathers is made good in the following season, whereas an injury to the wing-membrane of a Bat reduces the animal's capacity for flight for the rest of its life.

57–58. The principal flight feathers, or remiges, of the wing of a Bird (Mallard or Wild Duck, *Anas boscas*), showing their relations to the bones in the partially closed wing (57), and in the opened wing (58) (frontispiece, lower figure). The feathers that are attached to the bones of the hand (metacarpal and phalangeal bones of the second and third digits) are termed "primaries," those attached to the hinder bone of the fore-arm (ulnar bone) are known as "secondaries." Passing from quill to quill is a ligament which secures an even spacing of the feathers when the wing is opened. In the closed wing the quills of the feathers are set at a sharp angle to the bones of the fore-arm and hand, but as the wing is opened and the angle between the ulnar and metacarpal bones increases, the quills become more widely spaced, and become set more at right angles to the bones to which they are attached. This spreading out of the feathers is a consequence of the mode of linking of the bones of the wing and the mode of connection of the quills by the common ligament. It is independent of muscular action: the feathers can be spread out in a dead bird by merely straightening the skeletal parts of the wing.

59. Dissection of the middle part of the wing of a Bird (Bearded Vulture, *Gypaetus barbatus*), under view, to show the mechanism by which the "secondary" flight feathers are spread. Passing from quill to quill is a common ligament (A) which beyond the wrist is continued on to the quills of the "primary"

feathers (not shown in this dissection). In the closed wing there is but a small angle between the middle and further parts of the wing skeleton (fore-arm and hand respectively), and the secondary feathers make a sharp angle with the fore-arm, and lie close together (see preparations 57 and 58 of the flight feathers of the wing of the Mallard). When the wing is extended, the angle between the hand and the fore-arm opens; the common ligament, acting from the hand, pulls upon the secondary feathers, which being loosely hinged at their bases on the hinder bone of the fore-arm (ulnar bone) spread out, as in the opening of a fan, and stand nearly at right angles to the bone.

Attached to the under side of the quills of the secondary feathers are small tendinous extensions (B) from a muscle (C), a part of the *flexor carpi ulnaris*, which runs the whole length of the fore-arm. During the down-beat of the wing these tendons pull upon the quills, and prevent the whole sheet of flight feathers from being forced up into a vertical position. They do not serve to rotate the quills on their axes, as is sometimes stated.

60–61. Transverse section through the middle part of the wing of a Wood-Pigeon (*Columba palumbus*), including the basal

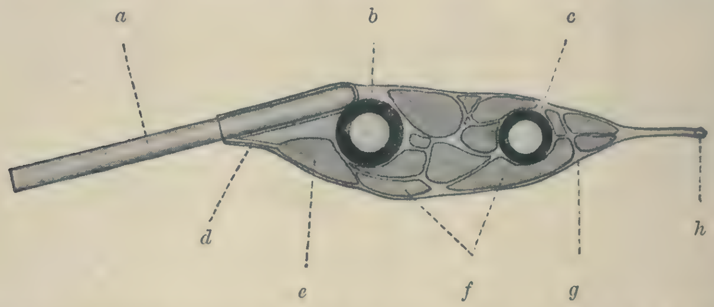

Fig. 19.—Transverse section through the middle part of the wing of a Wood-Pigeon (*Columba palumbus*) (see 60). *a*, quill of feather; *b*, ulna; *c*, radius; *d*, tendon; *e*, *flexor carpi ulnaris*; *f*, other muscles; *g*, skin; *h*, elastic ligament.

part of one of the secondary flight feathers, and an enlarged sketch. The preparation shows how the quill of the feather is supported at its basal extremity on the ulnar bone, and has attached to its under side, near the opening of the quill-pocket, a small tendon which arises from the side of the muscle known as the *flexor carpi ulnaris* (fig. 19). This muscle takes its origin

from the distal end of the humerus, and, after running beneath the ulnar bone for the whole of its length, is inserted by a tendinous extremity into the hinder of the two carpal bones. On contraction, this muscle becomes taut, and prevents the flight feathers from being forced upward by the air-pressure during the down-beat of the wing. It has been claimed, indeed, that the muscle by its contraction actually draws the feathers downward, and thus increases the concavity of the under surface of the wing. For another dissection of this muscle, see wing of the Bearded Vulture, 59.

62. Portions of feather set out in a manner to explain the rotation of the flight feathers which according to some authorities occurs during the up-beat of the wing. The pieces of feather in the upper row illustrate the slant assumed by the feathers when the wing is raised, those in the lower row represent the relations of the feathers during the down-beat of the wing. The flight feathers of the wing, particularly the "secondary" feathers (fig. 18, 2), are capable of a certain rotary or torsional movement about their axes. This movement is automatic, and is not due, as has been stated, to the action of small tendons proceeding from one of the muscles of the wing. During the up-beat of the wing, the broad part of the vane of each feather slopes down and the narrower part of the vane slopes up owing to the air pressure from above being greater on the former than on the latter. The wing thus rises easily through the air. When the wing is forcibly depressed, however, the air pressure being greater on the under side of the broad part of the vane than below the narrow part, the former is pressed up against the narrow part of the vane of the next feather, and the whole system of feathers thus forms an impervious sheet. The slight twist on the axis of the feather which is a necessary accompaniment of the changes above described is well within the limits of torsional elasticity of the axis. The specimens are shown in order to explain the views of certain authorities, but the subject is contentious, and there are those who maintain that the opening and closing of the feathers of the wing like the laths of a Venetian blind cannot take place, because during the up-beat the air cannot get beneath the narrow parts of the feathers to press upon the broad parts of the feathers which they overlap.

63. A flight feather of a Vulture (Bearded Vulture, *Gypaetus barbatus*), namely, one of the secondary feathers of the left wing.

From the main axis barbs project right and left. The proximal and distal edges of the barbs (i.e. towards the basal and apical ends of the feather respectively) bear innumerable barbules, too

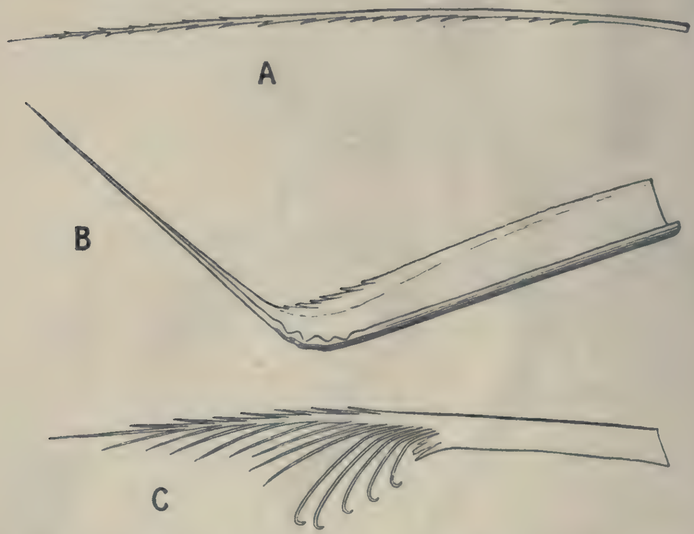

Fig. 20.—A, barbule of a feather of an American Ostrich, enlarged 42 diameters. Small spiny, or hairy, processes occur along the under edge and along a part of the upper edge (see microscope slide M). B, one of the proximal barbules of a wing-feather of a Bearded Vulture, i.e. a barbule taken from the side of a barb that is towards the base of the feather (see 63, C). Enlarged 136 diameters. The basal part of the barbule (towards the right in the figure) has an overturned scroll-like upper edge, the other part is sharply bent upon the basal part, and tapers off to a point. C, one of the distal barbules of a wing-feather of a Bearded Vulture, i.e. a barbule taken from the side of a barb that is towards the tip of the feather (see 63, D). Enlarged 136 diameters. The basal portion of the barbule (towards the right in the figure) is strap-shaped, the other part is broken up or shredded into bristle-like processes, a few of which (five in the specimen figured) end in hooks. These hooks of the distal barbules fasten over the scrolls of the proximal barbules, and thus impart a certain firmness to the vane of the feather (see microscope slide L). The barbule C is represented as flattened out; in the actual specimen the basal half is twisted upon the other half through nearly a right angle (see 63, B and D).

small to be seen by the unaided eye, but illustrated in the sketch A and the model B.

A. Enlarged sketch of the part indicated on the feather by the small square, to explain the position and relative size of the barbs and barbules represented in the greatly enlarged model B.

B. A greatly enlarged model (x 225) of the small portion of the feather indicated in the middle of the sketch A. The basal portions of the *proximal* barbules have scroll-like upper edges, and overlapping lower edges; the free ends of these barbules are very thin, and are bent at an angle to the basal portions, and overlap in planes at right angles to the plane of the feather. The basal portions of the *distal* barbules overlap one another in the plane of the feather; the rest of each barbule, which is at right angles to the basal portion, is cleft or shredded into numerous filaments, of which three, four or five on the under side are strongly incurved. The curved ends hook over the scroll-like upper edges of the proximal barbules—to avoid confusion, the actual hooking is not shown in the model. This locking of the two sets of barbules not only gives a stiffness to the vane of the feather, but also makes it possible for adjacent barbs to become hooked together again after having been forcibly separated. The resistance which the vane of the feather offers to the air is due to the overlapping of the basal portions of the distal barbules, and the overlapping of the lower edges of the basal portions of the proximal barbules.

C. Model of a single barbule of the proximal series, enlarged 225 diameters (fig. 20, B).

D. Model of a single barbule of the distal series, enlarged 225 diameters (fig. 20, C).

64. Feather of a flightless Bird (*Rhea americana*). The fluffiness of the feathers of flightless Birds such as the Ostrich, Rhea and Emu, as contrasted with the firmness of the vane of a feather of a Bird of strong flight, is due to the absence of hooks and scrolls upon the barbules; the barbules, proximal and distal, are all alike and have short spiny or hairy processes along the edges (see microscope slide M, and fig. 20, A). In flying Birds, on the other hand, the proximal and distal barbules are not alike, the former have scroll-like upper edges and the latter have some of the bristle-like projections on the under side ending in hooks. The hooks fasten upon the scrolls, and give to the vane a firmness which enables it to offer considerable resistance to the air (see 63, B; also microscope slide L, and fig. 20, B, C).

65. Dissection of a Bird (Wood-Pigeon, *Columba palumbus*), showing the two principal muscles of flight.

The muscle concerned in the depression of the wing is the *pectoralis major*. In this dissection the *pectoralis major* of the

Fig. 21.—Dissection of a Bird (Wood-Pigeon, *Columba palumbus*), showing the two principal muscles of flight. The right wing is thrown back, and the great breast muscle, the *pectoralis major* (A), has been cut close to its origin from the sternum, and turned aside, so as to expose the deep breast muscle, the *pectoralis secundus*, or *supracoracoideus* (B). The cut edges of the *pectoralis major* are marked C (see 65).

right side (A) has been cut close to its origin from the sternum (see the parts outlined in red), and thrown back so as to expose the *pectoralis secundus*, also known as the *supracoracoideus* (B), the principal muscle concerned in the elevation of the wing (see fig. 21). Compare with this dissection the skeleton of the Pigeon, 67, showing the areas of attachment of the pectoral muscles to the bones.

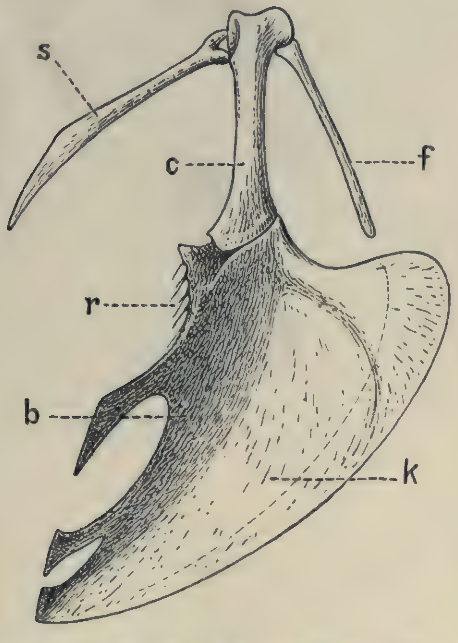

Fig. 22.—Sternum and Shoulder Girdle of a Pigeon (*Columba livia*), seen from the right side. *b*, body of the sternum; *c*, coracoid bone; *f*, furcula or merrythought; *k*, keel of the sternum; *r*, ends of the ribs connected with the edge of the sternum; *s*, scapular bone or shoulder blade.

66. Simple model to illustrate the mechanical principles involved in the elevating and depressing of the wing of a Bird.

The brass lever, representing the wing, is hinged upon a brass frame, the upper piece of which stands for the scapular bone. This piece is held against a board that occupies the position of the middle plane of the body by cords (white cords, representing the *trapezius* and other muscles), in order to suggest that this part of the mechanism can resist a pull but not a push. The stout lower piece (the equivalent of the coracoid bone) presses

against a block, but is not fixed to the block; it can resist a push, but not a pull. The third piece, a slender rod representing the clavicular bone, can resist a slight push and a slight pull, and this is suggested by its end being inserted into an eyelet in the board (see skeleton 67, and fig. 22).

The brass lever is actuated by two cords. The blue cord, standing for the *pectoralis secundus* muscle, is attached to the board at a part which may be considered as the equivalent of the keel of the sternum; it passes up between the two lower limbs of the brass framework (as the tendon of the *pectoralis secundus* muscle passes ventral to the coracoid and dorsal to the clavicular bone), it then traverses a guiding hole (*foramen triosseum* of the skeleton), and runs some distance along the grooved upper edge of the lever, and is tied at a point beyond the fulcrum. The red cord, standing for the *pectoralis major* muscle, is attached to the board just below the attachment of the blue cord, and is tied to the lower edge of the brass lever at a point beyond the fulcrum.

If the blue cord be tightened and the red cord slackened the lever rises; if the red cord be tightened and the blue cord slackened the lever is pulled down. The tightening and slackening of the cords find their equivalents in the bird in the contraction (shortening) and relaxation (release from shortening) of the muscles.

67. Skeleton of a Pigeon showing the attachments of the three pectoral muscles. The *pectoralis major* is the principal muscle concerned in the depression of the wing. One part of it (*a*) arises from the lateral portion of the sternum, another part (*b*) from the marginal portion of the keel of the sternum, and the third part (*c*) from the coraco-clavicular membrane and the edge of the clavicular bone. The muscle is inserted into the under side of a process at the front edge of the basal end of the humerus. The *pectoralis secundus* (also known as the *supra-coracoideus*), the principal muscle concerned in the elevation of the wing, arises from the sternum, and thins off into a tendon which passes through the *foramen triosseum*, and is inserted into the dorsal side of the basal end of the humerus. The *pectoralis tertius*, a small muscle which draws the wing downward and backward, arises from a small part of the side of the sternum, and from the side of the coracoid bone, and is inserted into the postero-ventral part of the head of the humerus.

68–69. Wings of a Pigeon, *Columba livia*, and a Golden Plover, *Charadrius pluvialis*, dissected to show the relations of two muscles of the fore-arm which are not attached to the bones of the fore-arm, but extend across both elbow and wrist joints.

The *Extensor carpi radialis longior* muscle (E. c. r. l.) arises from the humerus some little distance above the elbow joint. At its distal end it is continued into a tendon which passes along a groove over the end of the radius, and is inserted into the metacarpal bone of the first digit.

Since the elbow and the wrist of a bird flex in opposite directions, the muscle and its tendon are not long enough to admit of the elbow being extended while the wrist is flexed; there follows therefore an automatic action by which the wrist is straightened out when the elbow is straightened.

It may be stated in a general way that when a muscle passes over *two* joints, as in the present case, it can without loss of efficiency become converted into a ligament. Although there is no bird in which the e. c. r. l. muscle is tendinous for its whole length, yet in some birds the tendinous part is longer in proportion to the muscular belly than in others—*e.g.* Plovers, Swifts, Hawks and Owls, as compared with Pigeons and Fowls. That a non-muscular cord would serve the purpose is illustrated by the red cord in model 70.

Among the advantages gained by the conversion of "two-joint" muscles of the limbs into ligaments—perfect examples of which occur in the feet of the Horse and Mole—are the reduction of the weight of the limbs, and a centralising of the muscular tissue within the basal part of the limbs, or even in the body itself. The end joints of the limbs are thus worked by cords actuated by muscles near or in the trunk, and not by muscles situated in the middle parts of the limbs themselves.

A similar but much less efficient instance is afforded by the *Flexor carpi ulnaris* muscle (F. c. u.), which arises from the end of the humerus just beyond the articulation with the ulna, and is inserted into the ulnar carpal bone. For the explanation of its action see the blue cord in model 70. In these dissections the small tendons which pass from the f. c. u. muscle to the quill-pockets (59 and 60, and fig. 19, *d*) have been dissected away.

70. Model of brass and silk explaining the action of the "two-joint" muscles (shown in the dissections 68 and 69), on the

supposition that they have been completely converted into ligamentous cords. When the angle between A (= humerus) and B (= radius and ulna) is opened out, the piece C (= bones of the hand) becomes straightened upon the piece B by the pull of the red cord (representing the *Extensor carpi radialis longior* muscle). When the piece A folds over upon B, the piece C is drawn down by the action of the blue cord (representing the *Flexor carpi ulnaris* muscle).

71. Simple model, constructed of strips of card and drawing-pins, explaining the action of the link-work of the bones of a Bird's wing. The strips are marked "hand," "radius," "ulna," "humerus." When the humerus is moved over to the left, so as to reduce the angle which it makes with the ulna, it pushes the radius to the left and causes the hand to bend down.

72–75. Wings of Gannet, *Sula bassana*, Peregrine Falcon, *Falco peregrinus*, Megapode, *Megapodius nicobaricus*, and Wild Turkey, *Meleagris gallopavo*, to show the differences in shape. In a general way birds of strong and prolonged flight, and birds which remain for long periods on the wing, sparing their energy at times by soaring, have longer and narrower wings than those which are slow and clumsy fliers. Birds which flutter for short distances usually have wings which are roughly as broad as long. Such birds may be very strong fliers for short distances, but they do not remain long in the air. Ordinary migratory birds have wings of intermediate pattern between the two extremes shown.

76–77. Wings of two nearly related Warblers (fig. 23), the migratory Sedge Warbler of Europe (*Acrocephalus phragmitis*) and a non-migratory Warbler of British East Africa (*Cisticola chineana*), and the wings of two Quails, the migratory Common Quail of Europe (*Coturnix coturnix*) and the non-migratory Florida Quail (*Ortyx floridanus*). The generalisation that birds which are good fliers usually have long, pointed wings, whereas poor fliers have blunt-ended or rounded wings (72–75), is of exceptional interest in connection with closely allied species of bird, of which one is migratory in habit whereas the other is sedentary. In the two examples shown the non-migratory bird happens to be larger than the migratory bird, but attention is drawn to the shape, and not to the size of the wings. The wing of the non-migratory bird is rounded at the extremity, whereas

that of the migratory bird is proportionately longer and more pointed. Similar examples might be shown from among the Pigeons, the Thrushes and the Owls.

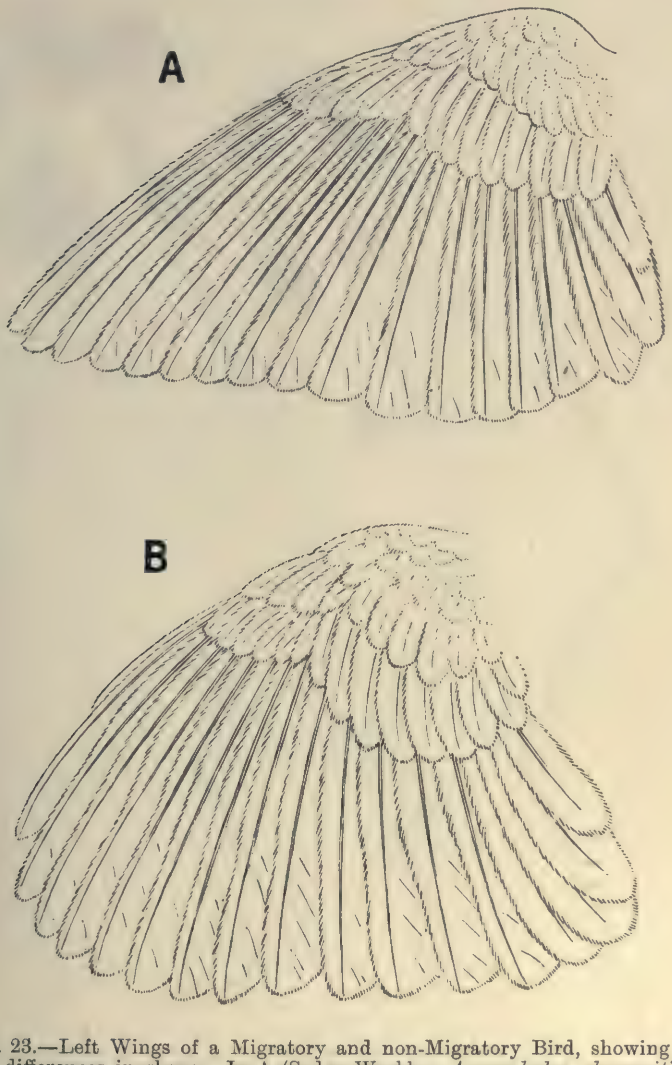

Fig. 23.—Left Wings of a Migratory and non-Migratory Bird, showing the differences in shape. In A (Sedge Warbler, *Acrocephalus phragmitis*, a migratory bird) the wing is comparatively long and pointed ; in B (a non-migratory Warbler of British East Africa, *Cisticola chineana*) the end of the wing is rounded (see 76).

78. Diagram showing the relative lengths of the three parts of the wing skeleton in the Gannet, Pigeon and Swift (fig. 24). The wing bones shown in preparation 79 illustrate an interesting

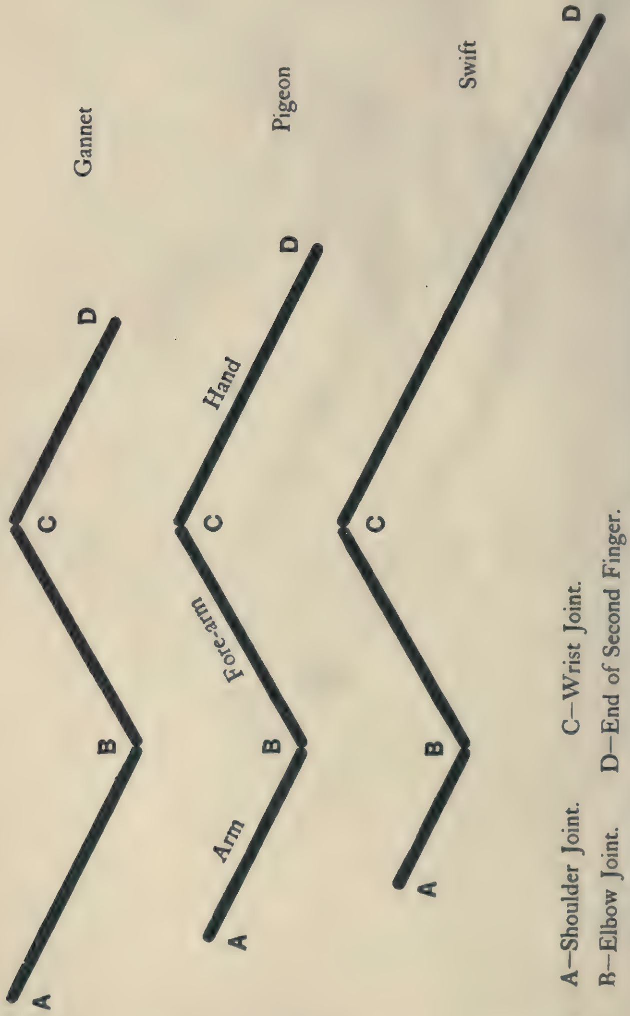

Fig. 24.—Diagram showing the relative lengths of the three parts of the Wing in the Gannet, Pigeon and Swift. (For explanation see 78.)

difference in the proportions of the first, second and third parts of the wing—the arm, fore-arm and hand respectively. The Gannet, Pigeon and Swift are all birds of strong flight, yet in the Gannet

the humerus is longer than the ulna and the ulna longer than the second finger (metacarpal and two phalanges); in the Pigeon the humerus is shorter than the ulna and the ulna shorter than the second digit; in the Swift the humerus is short as compared with the ulna and the hand is remarkably long. Taking the fore-arm as of the same length in all three, the relative lengths of the first part of the wing (from shoulder joint to elbow joint), the second part (from elbow joint to wrist joint), and the third part (beyond the wrist joint) are as represented in the diagram (fig. 24). In the Pelican both the humerus and the hand are shorter than the ulna. In Ratite birds, in which the wing has become reduced, the reduction is much more marked in the fore-arm and hand than in the humerus.

79. Skeleton of the right wings of the Gannet, *Sula bassana*, Pigeon, *Columba livia*, Swift, *Cypselus apus*, Hoatzin, *Opisthocomus hoazin*, and Fulmar Petrel, *Fulmarus glacialis*, showing the differences in the pneumaticity of the bones. In Birds the air-sacs which project from the lungs are continued not only between the viscera, but also to a greater or less extent into the interior of the bones, particularly the sternum, the coracoid and the vertebrae; the air-sacs penetrate to a varying extent into the bones of the wing. Bones so invaded by the air-sacs are said to be "pneumatic." In the Gannet all the bones of the wing are pneumatic; in the Albatros, Swift and Pigeon the humerus is pneumatic, but not the other bones of the wing; in the Fulmar Petrel, Cape Pigeon, Divers, Darters, Cormorants, etc., none of the wing bones are pneumatic. It was formerly stated that the pneumaticity of the bones had the effect of reducing the weight of the bones without reducing their strength, and so served to render the flight of the bird more efficient. As will be seen, however, from the instances mentioned above, the extent of the pneumaticity of the bones is not directly connected with the power of flight, for the birds in question are all strong fliers. On the other hand, the Hoatzin, which scarcely flies at all, but clumsily flutters from tree to tree, has bones which in their pneumaticity agree with those of the Albatros and Swift. And the flightless birds, such as the Ostrich, have bones which in their pneumaticity are not inferior to those of some of the best fliers. In a roughly prepared skeleton of a bird the non-pneumatic bones can usually be distinguished from the pneumatic bones by their yellow colour and greasy appearance.

80. Humerus and ulna of the Albatros, *Diomedea exulans*, cut longitudinally to show the internal cavities. The interior of the humerus is occupied in life by air, that of the ulna is filled with a fatty marrow. Bones of the former kind are termed "pneumatic," those of the latter kind "non-pneumatic" (see 79).

81. Left wing of a Pigeon, *Columba livia*, seen from the under side. The humerus and ulna have been cut open to show the air-sac in the former and the marrow in the latter.

82. Series of sterna and shoulder girdles of fifteen Birds.

The sternum of Birds consists of a bony body or plate, more or less horizontally disposed in the bird as it flies, and a keel, a thin lamella of bone which projects downward from the middle of the plate, and lies in the median plane of the bird's body (fig. 22).

The shoulder girdle consists of a pair of coracoid bones, articulated with the front part of the sternum, a merrythought or furcula, representing a pair of clavicular bones, and thirdly, a pair of shoulder blades or scapular bones, not shown in the majority of the specimens of the present series. The first or basal bone of the wing, the humerus, articulates at the junction of the coracoid and scapula.

The keel of the sternum is relatively most extensive in birds of strong flight, and is wanting in the Apteryx (O), Emu (P), and other flightless birds. These latter, indeed, are termed "Ratitae," because in them the sternum resembles a raft, a flat structure without a keel below. In the Parrot *Stringops* the keel of the sternum is very small.

In some birds, such as the Gannet (K), Cormorant (C), and Penguin, the keel projects well forward; in the Divers, Cormorant (C) and Gannet (K), it does not extend on to the hinder part of the plate; in the exceptional Hoatzin (M) the keel is confined to the hinder half of the plate of the sternum. In the Albatros (J), Petrel, Frigate-bird (B), Ostrich and Apteryx (O), the plate or body of the sternum is scarcely longer than it is wide; in Eagles (A), Geese (H), and Divers it is rather long and parallel-sided; in the Trumpeter (E) and Rail (L), it is much longer than broad; indeed, in the latter the sternum consists of scarcely more than the keel.

In the Pigeons (N) the plate of the sternum is incised behind, and in Game Birds (D), Rails (L) and Tinamous (F) it is deeply incised. The incised regions are in the living bird closed by membrane, and to this as well as to the bony parts the pectoral

muscles are attached; so that an incised sternum does not necessarily signify reduced powers of flight. Of the birds mentioned the Pigeons may be classed as strong fliers, the Game Birds as powerful fliers over short distances, and the Rails and Tinamous as feeble fliers.

The furcula is slender in the Rails (L) and Tinamous (F), but equally so in the Pigeons (N). It is rather weak in both Game Birds (D) and Swifts, but it is thick and strong in the Swans, Screamers and Adjutant (G). In birds of vigorous flight, such as Eagles (A) and Falcons, and birds of powerful sustained flight, such as the Albatros (J), the furcula has its two upper ends wide apart, and it is curved in such a way that in a side view the anterior edge is convex. A similarly curved furcula occurs in the Penguins, which do not fly at all. The furcula is reduced in the Emu, Cassowary and some Parrots; it is wanting in the Apteryx (O), Ostrich and Rhea, and in *Mesites*, a curious thrush-like bird of Madagascar. The hind part of the furcula may for increased steadiness be movably articulated with the front of the keel of the sternum, as in the Gannet (K), or connected with it by ligament, *e.g.* the Adjutant (G), Cormorant (C), Petrel and Albatros (J), or fused with it, as in the Pelican, Crane and Frigate-bird (B). The hind end of the furcula is produced into a hypocleideum in some birds (*e.g.* Game Birds (D)), but this is not united with the sternum. The upper end of the furcula has an articulation with the coracoid in the Pelican, Cormorant (C), Gannet (K), Eagle (A) and Falcon; it is fused with the coracoid in the Frigate-bird (B) and Hoatzin (M).

The coracoid bones are short and broad in the Albatros (J) and Petrels, and have lateral articulations with the sternum in addition to the ordinary articulations. The coracoids are also rather short and broad in the Divers, Eagles (A) and Falcons; they are proportionately long and stout in the Adjutant (G), Pelican, Frigate-bird (B) and Penguin. The sternal ends of the two coracoid bones usually come close together, but they are widely separated in some of the Ratite Birds (O).

On reviewing the skeletal features above recorded it will be seen that there is apparently but little correlation between them and the habits of the birds in question. Different soaring birds do not necessarily agree in the proportions of the sternum and shoulder girdle, and the same may be said of rapid fliers, diving birds, running birds, and birds which turn sharply in the air (such as Frigate-birds and Falcons). One may say that among

allied birds the more powerful fliers have more extensive keels to the sterna than the poor fliers. In birds of strenuous flight, capable of turning rapidly in the air and striking their prey with force, there is usually a concentration of the breast muscles far forwards, and either a lengthening of the coracoids and the sternum, or else a shortening of the coracoids and a widening of the distance between the two ends of the furcula.

Only a few examples of sterna are shown here; a larger collection is to be seen in the South Wall-case in Bay III. of the Entrance Hall.

A. Golden Eagle, *Aquila chrysaetus.* The body of the sternum is parallel-sided. The upper ends of the furcula are wide apart, and are movably articulated with the upper ends of the coracoid bones.

B. Frigate-bird, *Fregata aquila.* The sternum is short and wide. The furcula is fused with the coracoid bones in front and the keel of the sternum below.

C. Cormorant, *Phalacrocorax carbo.* The keel of the sternum projects well forward, and is attached by ligament to the back of the furcula; the keel does not extend over the hinder part of the body of the sternum. The furcula is movably articulated with the upper end of the coracoid.

D. Capercaillie, *Tetrao urogallus.* In the Game Birds the body of the sternum is deeply incised behind. The point of the keel does not reach the level of the front of the body of the sternum. The furcula is produced behind into a process, called the "hypocleideum," but this is not connected with the keel of the sternum.

E. White-winged Trumpeter, *Psophia leucoptera.* The body of the sternum is long, narrow and parallel-sided.

F. Rufescent Tinamou, *Rhynchotus rufescens.* The body of the sternum is deeply incised behind, and the keel is of fair extent. The furcula is greatly reduced.

G. Adjutant, *Leptoptilus dubius.* The sternum is small in comparison with the furcula and coracoid bones. The furcula is connected by ligament with the front of the keel of the sternum.

H. Spur-winged Goose, *Plectropterus gambensis.* The body of the sternum is long and parallel-sided, and fenestrate in its hinder part.

J. Albatros, *Diomedea exulans.* The body of the sternum is wide and short, and the keel not very extensive. The coracoid is short and broad, and articulates with the sternum by two facets.

The furcula is connected with the front of the keel of the sternum by ligament; its upper ends are wide apart.

K. Gannet, *Sula bassana.* The keel of the sternum projects well forward, and is movably articulated with the back of the furcula; the keel does not extend over the hinder part of the body of the sternum. The furcula is movably articulated with the upper end of the coracoid.

L. Clapper Rail, *Rallus longirostris.* The body of the sternum is long and very narrow, and deeply incised behind; the keel is large. The furcula is slender.

M. Hoatzin, *Opisthocomus hoazin.* The Hoatzin, a bird of the Amazon valley, scarcely ever flies, but flutters clumsily from branch to branch and from tree to tree, and is rarely seen on the ground. The sternum is remarkable in that the front part of the keel is absent, a feature correlated with the reduction of the muscles of flight, and partly with the weight of the greatly increased food-pouch or crop. The furcula is Y-shaped, and fused in front with the coracoid and behind with the sternum.

N. Pigeon, *Columba livia.* In Pigeons the body of the sternum is either fenestrate in its hinder part or incised; the keel is large (fig. 22). The furcula is slender, and the upper ends are comparatively close together.

O. Shaw's Apteryx, *Apteryx australis.* The Kiwis, or various species of *Apteryx*, are the smallest of the Ratite Birds, and are restricted to New Zealand. The sternum is broad and without a keel. The sternal ends of the coracoid bones are wide apart. The scapula is fused with the coracoid, and there is no furcula.

P. Emu, *Dromaeus novae-hollandiae* (young). The Emus, or various species of *Dromaeus*, are Ratite Birds of Australia. The sternum is thick and without a keel. The scapula fuses with the coracoid in the adult; there is only a vestige of a furcula.

83–84. Sterna of the migratory Sedge Warbler of Europe (*Acrocephalus phragmitis*) and a non-migratory Warbler of British East Africa (*Cisticola chineana*). The sternum is relatively larger in the former than in the latter bird, the flight muscles attached to the sternum being more largely developed in the migratory than in the non-migratory species. (The sterna are from the same species as those from which the wings shown in preparation 76 were taken.)

85. Diagrams of the skeleton of the left fore-limb of a Man, a Bat, a Pterodactyle and a Bird, showing that, while the pro-

portions differ considerably, the essential construction of the limb skeleton is the same in all. The humerus is coloured blue, the radius and ulna red, the carpal bones green, and the metacarpal bones and phalanges yellow. Equivalent digits are denoted by similar numerals. (In order to economise space the fifth digit of the Pterodactyle is drawn in the flexed position.) See frontispiece, the upper figure of which is a photograph of the remains of the wing of *Rhamphorhynchus gemmingi* from the Lithographic Stone of Eichstädt, Bavaria, the middle figure a photograph of the wing of a Long-eared Bat, *Plecotus auritus*, the lower figure a photograph of the wing of a Duck, *Anas boscas*, after removal of the smaller feathers, or coverts.

86. Restoration of *Archaeopteryx;* natural size. *Archaeopteryx* is a genus of extinct Birds—the most ancient Birds of which any record is known. Two skeletons, with impressions of feathers, have been obtained from the Lithographic Stone (Kimmeridgian) of Solenhofen, in Bavaria. One of these is in the Geological Department of this Museum, the other is at Berlin. The vertebral axis of the tail of *Archaeopteryx*, instead of being shortened up as in all existing Birds, is long and lizard-like, with the rectrices or principal tail-feathers arranged regularly along the two sides (fig. 25). The bones of the wing and leg differ but little from those of modern Birds; the three digits of the wing end in curved claws. The three digits did not project freely from the front of the wing like the front fingers of a Pterodactyle: many of the published restorations of *Archaeopteryx* are incorrect in this respect. The skull is bird-like in shape and general constitution, but both upper and lower jaws bear teeth.

87. Restored sketch, of the natural size, of the tail of *Archaeopteryx*, showing the relation of the principal tail-feathers (rectrices) to the vertebrae (fig. 25). In *Archaeopteryx* the caudal skeleton is not shortened up as it is in other Birds. The number of caudal vertebrae fused with the sacrum is doubtful, but probably not more than four. Then follow four vertebrae which have short plate-like transverse processes for the attachment of muscles. The remaining vertebrae are fifteen in number, and each supports at its anterior end a pair of the tail-feathers. The last vertebra is long and slender, and lies in the same line with the others; there is no fusion of the terminal vertebrae to form a pygostyle such as occurs in other Birds. In the sketch the principal tail-feathers alone are shown; in all probability the

basal quills of these feathers were covered above and below by small feathers, the tail-coverts, but there is no evidence of them in the fossil remains at present known. In contrast with the large number (15 pairs) of tail-feathers in *Archaeopteryx* it is to be noted that in modern Birds the usual number of rectrices is six pairs; the Common Snipe, however, has seven pairs, and the Great Snipe eight pairs, while in *Gallinago stenura* there are as many as ten pairs.

88–89. Tails of Wood-Pigeon, *Columba palumbus*, showing the principal feathers (rectrices) closed and spread. The quills of the rectrices arise close together at the sides of the ploughshare bone or pygostyle, and not at intervals along the sides of a vertebral axis as in *Archaeopteryx* (fig. 25). The feathers, therefore, while setting more or less parallel when the tail is closed, radiate when the tail is opened.

90. Dissection of the pelvis and tail of a Pigeon, *Columba livia*, showing the two muscles which are principally concerned in the opening out of the rectrices or large feathers of the tail. The muscle seen on the right side at *A* is the *pubi-coccygeus*, also known as the *adductor caudae*. It arises from the hinder part of the pubic bone, and is inserted into the sheath of the outermost tail-feather. On the contraction of the muscle this feather is drawn downward and outward, and the other feathers (excepting the innermost) follow, being connected by an elastic ligament at the mouths of the quill-sheaths. The muscle seen on the left at *B* is the *levator coccygis*, also known as the *levator caudae*. Its effect, on contraction, is to draw the basal end of the outermost feather upward, forward and inward. The upward pull counteracts the downward pull of the *pubi-coccygeus* muscle. The forward and

Fig. 25. — Tail of *Archaeopteryx*, showing the relation of the principal feathers (rectrices) to the vertebrae. The small covering feathers (coverts) are not shown (see 87).

inward pull on the basal end of the outer feather has the effect of directing this and the adjoining feathers somewhat outward. Compare with this dissection model 91.

91. Simple model to illustrate the mode of opening and closing of the tail of a Bird. The tail consists usually of six principal feathers on each side of the middle plane. The basal ends of the feathers are held together by connective tissue in such a manner that, while a certain amount of radiating movement is possible, the bases of the feathers do not separate. This is suggested in the model by the card strips (representing the quills of the feathers) being pinned in a movable manner upon a short strip of wood. The strip of wood is movably pinned at the end near the red line, but is otherwise free. At some distance along the strips of card from their pinned ends a piece of elastic passes across the series, and is stitched to each by a green thread. This piece of elastic is the equivalent of the elastic ligament which in the bird passes from quill to quill, and secures the even spacing of the feathers when the tail is opened. The piece of elastic is fixed at the inner end (near the red line), but at the outer end is tied to a blue cord, which passes outward and upward (*i.e.* forward in the bird) and is tied to a brass eyelet. When the blue cord is tightened, the elastic stretches, the strips of card open out in a radiating manner, and the strip of wood to which the cards are movably pinned moves round. When the blue cord is slackened, the elastic shortens, the card strips close up and are drawn parallel to the red line. The tightening and slackening of the blue cord represent the contraction and relaxation of the *pubi-coccygeus* and *levator coccygis* muscles of the bird, which are attached to the sheaths of the outermost feathers of the tail, and pass forward to be attached to parts of the skeleton. See dissection 90.

92. The hindermost portion of the vertebral column and the pelvic girdle of a Wood-Pigeon, *Columba palumbus*, seen from the dorsal aspect. In Birds the mass of fused vertebrae constituting the sacrum (or synsacrum) is exceptionally large. The number of vertebrae included varies in different birds; in the present instance there are fourteen vertebrae, consisting of the last thoracic, the lumbar and sacral vertebrae and some caudal vertebrae. The next six caudal vertebrae are free and movable, and the series is terminated by an uptilted bone known as the pygostyle, which represents a number of coalesced vertebrae.

It is to the right and left sides of the crest of the pygostyle that the innermost pair of tail-feathers are attached.

93. The hinder portion of the vertebral column, and the pelvic girdle, of a young Fowl, two days after hatching. Under side.

94. An enlarged sketch of the last twelve elements of the vertebral column of a young Fowl, two days after hatching (93). The four vertebrae marked A become the free or movable caudal vertebrae of the adult, the last six elements (B) fuse up to form the pygostyle.

95. The last five pieces of the vertebral column of an adult Fowl. Left side. A, the four free caudal vertebrae; B, the ploughshare bone or pygostyle, formed by the fusion of six bones which are separate in the young. (In some individuals there are five free caudal vertebrae, and the pygostyle then includes five bones only.)

96. The last five pieces of the vertebral column of a younger Fowl, showing the component parts of the pygostyle not yet completely fused. Left side.

INVERTEBRATES OTHER THAN INSECTS.

It is worthy of remark that the only animals that really fly are either Vertebrates or Insects. The only Invertebrates other than Insects that are of interest in the present connection are the Parachuting Spider, the young spiders of many species that float about by means of their gossamer threads, and the so-called Flying Copepods.

Fig. 26.—The Parachuting Spider, *Saitis volans* (*Attus volans*), of New South Wales. The spider is one-sixth of an inch in length.

From O. P. Cambridge, "On some new Genera and Species of Araneidea," *Ann. Mag. Nat. Hist.* ser. 4, vol. xiv, No. 81, 1874, pl. XVII, fig. 4.

97. Enlarged drawing of the Parachuting Spider, *Saitis volans* (*Attus volans*), of New South Wales (fig. 26). This spider is a small jumping spider, with the lateral edges of the abdomen expanded into plates which, by acting as a parachute, enable the animal to take exceptionally long leaps. When at rest the

lateral flaps are bent downward. The spider is rare, and only males are known.

98. A Spider, *Celaenia excavata*, female, with its cocoons, and the young spiders removed from one of the cocoons. In this and most spiders the young, on hatching out in the summer and autumn, resort to a "ballooning" habit which secures their dispersal far and wide. The young spider climbs to the top of a stalk and faces the wind. Raising the body by stiffening its legs, it exudes one or more fine threads (gossamer threads) from the spinnerets at the end of the abdomen and allows them to float away freely into the air (fig. 27, A). When the threads are sufficiently long the spider lets go its grip, and is carried away by the wind. It floats passively, with its upper side undermost (fig. 27, B, C), until a suitable stopping-place is reached. The descent is then controlled by the spider gathering in the filaments with its front legs and rolling them up on the under side of the body (fig. 27, D)

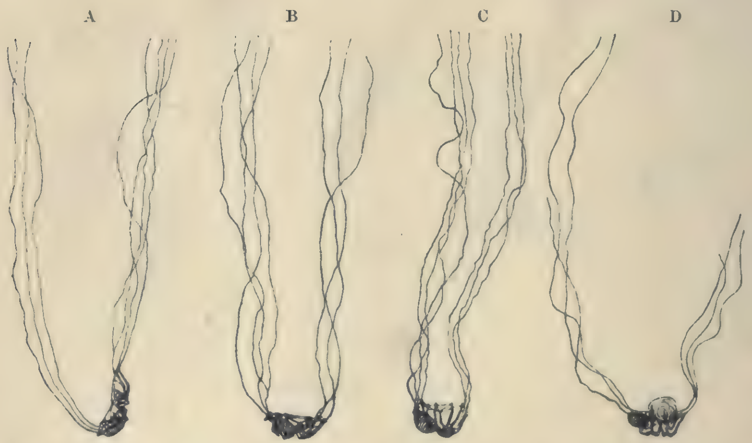

Fig. 27.—Enlarged sketches of young Lycosid Spiders floating by means of their gossamer threads. A, attitude of the spider just after taking flight; B and C, attitude when floating in the breeze; D, attitude of the young spider gathering in its threads for descent.

From H. C. McCook, *American Spiders*, vol. ii, 1890, pp. 260, 261.

until the general buoyancy is lessened, enabling the spider to float down to the ground in the selected area. More often, however, the spider is brought up by contact with the foliage of a tree. The speed of the "flight" is of course determined by the force of the wind, and the distance covered is inversely as the amount of

obstruction encountered.* Sometimes the several threads of the same spider or the threads of several spiders become entangled into a flocculent mass or "mop," which is blown through the air until the young spiders decide to alight, when they hang down from the "mop" by single threads and separate themselves from it.

99. Enlarged sketches of young Lycosid Spiders floating by means of their gossamer threads (fig. 27).

100. Flying Copepods, *Anomalocera patersoni*, and an enlarged sketch. At least three forms of oceanic Copepod Crustacea † have been described as "Flying Copepods." They cannot, however, do more than spring out of the water and fall back again. They are of small size ($\frac{1}{8}$ inch in length), and occur in great swarms. In calm weather frequently the surface of the sea appears disturbed, as if by fine rain, owing to the emergence and re-entry of these crustaceans. In structure the Flying Copepods do not differ materially from others which have not the habit of springing into the air.

CASE 3.

INSECTS.

The wings of Insects are outgrowths from the second and third segments of the middle part of the body (thorax), and arise between the edge of the back (notum) and the side wall (pleuron) of the body (see diagram 108). They consist of two layers of very thin skin covered with the hard flexible substance (chitin) that forms the outer shell of the body of Insects, and between these two layers of the wing there run tracheal tubes for breathing and fine blood-vessels. The soft hinge membrane at the base of the wing may include a number of small pieces of hard chitin, which render the hinge-joint very complex.

No Insect has more than two pairs of wings.‡ In some

* A detailed account of the dispersal of young spiders by means of their gossamer threads is given by H. C. McCook, "American Spiders and their Spinningwork," vol. ii, Philadelphia, 1890, pp. 256–282.

† *Pontella atlantica*, *Pontellina mediterranea*, *Anomalocera patersoni*.

‡ Certain extinct Insects from the Carboniferous formation had flattened movable outgrowths like small wings projecting from the first segment of the thorax, and some modern Moths (*e.g.* the Owl Moths) have some movable plates, known as the patagia, attached to the "collar," or reduced prothoracic ring.

Insects (*e.g.* Beetles) the front pair are hardened and are not used for flight, but act as protective coverings for the second pair when the Insect is not flying. In some other Insects (*e.g.* Flies) the second pair of wings are reduced to small, stalked balancers or poisers (halteres). In others, again (*e.g.* Fleas and Spring-tails), both pairs of wings are wanting.

While the wings of Birds, Bats and Pterodactyles are the pectoral limbs modified for purposes of flight, the wings of Insects are not modified limbs, but are outgrowths of the dorsal plates (tergites) having no connection with the legs.

101. The front wings of a Moth (Emperor Silk-Moth, *Attacus vesta*) prepared to show that the wing of an Insect is composed of two separable layers. The left wing has been completely divided into its two component layers, the right wing is only partially split.

102. An American Locust, *Dissosteira carolina*, together with an enlarged sketch of the right fore and hind wings showing the complexity of the hinge-system.

WING MUSCLES OF INSECTS.

In Insects the muscles which move the wings are very numerous and complicated, and in the series of specimens here exhibited the muscles which are concerned with the straightening out, the folding up, the drawing forward, the drawing backward, and the alteration of the antero-posterior slope of the wing are disregarded, and only the larger muscles, those concerned with the elevation and depression of the wing, are illustrated and explained. The elevator and depressor muscles are of two kinds, direct and indirect. In the Dragon-flies the direct muscles are the principal muscles concerned, in Locusts and most Orthoptera the direct and indirect muscles are equally developed, but in most Insects (Beetles, Butterflies, Flies, Wasps, etc.) the direct muscles are feebly developed, and the indirect muscles are the largest in the whole body.

Direct Muscles of the Wings of Insects.

The direct muscles which raise the wings and those which depress them are vertically disposed muscles, attached at their lower ends to the sternal (lower) portion of the exoskeleton, near the

bases of the legs, and attached at their upper ends to the bases of the wings, or to small separate hard parts close to the bases of the wings. The hinge of the wing upon the body is extremely complex in structure, but from a mechanical point of view there can be recognised what is practically a single fulcrum. The elevator muscle is connected with the very short arm of the lever on the internal side of the fulcrum, *i.e.*, on the side nearer the middle of the body; the depressor muscle is connected with the long external arm of the lever (the wing itself), close up to the fulcrum. The mechanical principles involved are explained in model 103. The direct muscles of the wings are well developed in the Libellulidae (Dragon-flies), moderately developed in the Orthoptera, and only feebly developed or wanting in most Insects.

103. Flight Mechanism of Insects (Direct Action).—Simple model to illustrate the mechanical principles involved in the elevating and depressing of the wing of an Insect by the action of the direct muscles.

The brass lever, representing the wing, is hinged upon a curved piece of steel clock-spring which stands for the outer casing (chitinous exoskeleton) of the body of the Insect. The lever is actuated by two cords. The blue cord, standing for the direct elevator muscle, is attached to the lower part of the clock-spring (the part coloured green, and representing the sternum of the Insect); the upper end of the cord is tied to the lever at its inner end, that is, at a point nearer to the board than the fulcrum. The red cord, standing for the direct depressor muscle, is attached to the lower part of the clock-spring, and at its upper end is tied to the lever slightly beyond the fulcrum. When the blue cord is tightened and the red cord slackened, the lever rises; when the red cord is tightened and the blue cord slackened, the lever is drawn down.

Indirect Muscles of the Wings of Insects.

The indirect muscles which raise and depress the wings are not immediately connected with the wings, but are attached at both ends to the exoskeleton of the thorax, which being flexible can be altered in shape by their contraction, and in consequence of the change of curvature the wing is raised or lowered. The depressor muscle is disposed longitudinally in the body, and is attached at both fore and hind ends to downward continuations of the notum, or dorsal part of the exoskeleton, of the particular

somite (either the second or third thoracic) to which the wings belong. When the downwardly directed plates are approximated by the contraction of the great muscle which connects them, the notum above this muscle becomes more convex, and thus rises in its middle part. The rising of the middle part of the notum lifts the short inner arm of the lever, which has its virtual fulcrum at the junction of the notal (back) and pleural (side) portions of the exoskeleton; the long arm of the lever, the wing itself, is consequently lowered.

The elevator muscle runs vertically, or nearly so, and connects the notal (upper) and sternal (under) portions of the exoskeleton; and, since the sternum is more rigid than the notum, the contraction of the muscle has the effect of flattening the latter. The drawing down of the middle part of the length of the notum depresses the short arm of the lever, and consequently raises the long arm, or wing itself.

The mechanical principles involved are explained in model 104.

The indirect muscles are well developed in most Insects; they are moderately developed in Orthoptera, and very feebly developed or wanting in the Dragon-flies.

104. Flight Mechanism of Insects (Indirect Action).—Simple model to illustrate the mechanical principles involved in the elevating and depressing of the wing of an Insect by the action of the indirect muscles.

The brass lever, representing the wing, is hinged upon the upper end of the rigid part of the model, coloured yellow and green, and representing the pleuron and sternum respectively of the exoskeleton of the Insect. The curved piece of clock-spring (representing the notum of the Insect) fits at its edge into a notch in the short arm of the lever, and while free from the board (representing the middle plane of the body), works upon a guiding rod that is firmly attached at its middle to the yellow piece.

The lever is actuated by two cords, neither of which is tied to the lever. The blue cord is attached below to the rigid green piece and at its upper end to the middle of the clock-spring. The red cord is attached at its ends to the descending parts of the clock-spring. When the red cord is tightened and the blue cord slackened, the clock-spring becomes more curved, its upper, middle part is raised, the short arm of the lever is consequently raised, and the long arm is lowered. When the blue cord is tightened and the red cord slackened, the upper middle part of

the clock-spring is drawn down, the short arm of the lever also is drawn down, and the long arm rises.

105. Dissection of a Dragon-fly, *Aeschna cyanea*, with the side wall of the thorax removed to show the chief muscles of the wings. Of the four muscles seen the first and third draw the two

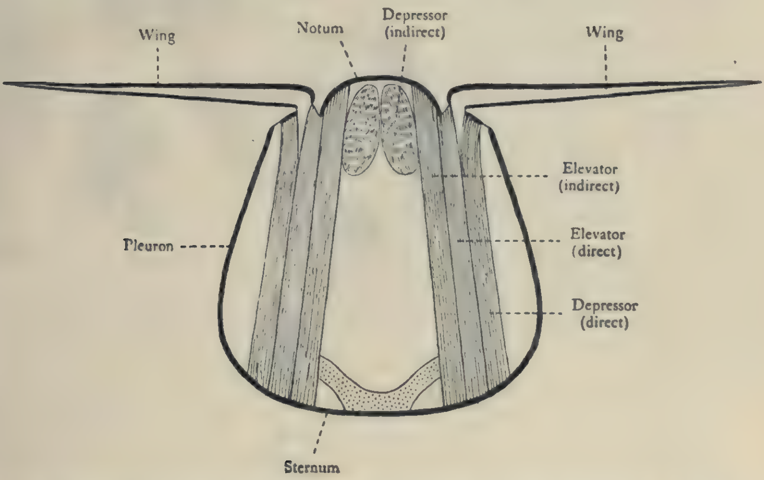

Fig. 28.—Diagrammatic sketch of a section across the thorax of a Locust, showing the principal muscles concerned in the elevation and depression of the wings (see 108).

wings forward, the second and fourth draw them downward. The elevator muscles lie deeper, and are not shown in the dissection.

106. Dissection of a Goliath-Beetle, *Goliathus giganteus*, with all the internal parts removed except the muscles of the wings. In the upper dissection the indirect elevator muscle of the wing is seen extending horizontally between two vertical skeletal plates projecting downward from the back (notum). In the lower dissection the indirect elevator muscle has been removed, and the vertically disposed indirect depressor muscle of the wing is seen extending from the notum to the sternum. The lower part of the indirect elevator muscle is also seen in the upper dissection. Small direct elevator and depressor muscles of the wing are present in Beetles, but in these dissections they are concealed from view by the great indirect muscles.

107. Dissection of a Locust, with the hind thoracic segment (metathorax), together with the second pair of wings and the third pair of legs, separated from the rest of the body, and showing the principal muscles of the wing. See explanatory sketch 108.

108. Diagrammatic sketch of a transverse section through the metathorax of a Locust, showing the four principal muscles of the wings (see fig. 28).

CHARACTERISTICS OF THE WINGS IN THE DIFFERENT ORDERS OF INSECTS.

Butterflies and Moths (Lepidoptera).

In Lepidopterous Insects both the front and hind wings are developed as organs of flight, and they are invested with closely disposed minute scales which give a fur-like or velvety appearance to the surface.

109. A Hawk-Moth, *Pseudosphinx tetrio*, after removal of the scales from the wings of the left side. The wing-membrane so prepared is as clear and its venation as distinct as in the wings of Flies and Dragon-flies.

110. An enlarged sketch ($\times$ 150) of three scales removed from the same Moth. The scales are flat, with longitudinal striations; they are attached to the surface of the wing by a kind of short stalk, while the free edge of the scale is broad and toothed. See slides F, G and H under the microscope, and fig. 42.

111–112. Two Clear-wing Hawk-Moths, a British species, *Hemaris* (*Haemorrhagia*) *fuciformis*, and a South African form, *Cephonodes hylas*. In Clear-wing Moths the scales of the wings resemble those of other Moths at the time that the insect emerges from the pupa-case, but they are fugitive, and most of them are shaken off during the first few flights.

113–114. Male and female of a large Butterfly, *Troides* (*Ornithoptera*) *priamus urvillianus*, from the Solomon Isles. The male is brightly coloured, while the female is dull. The female is a slower flier than the male, and has a larger expanse of wing; this is doubtless related to the fact that the female is weighed down by the mass of unlaid eggs in the body.

115–116. A Moth, *Urania leilus*, and a Butterfly, *Papilio policenes*, in which the hind wings are produced backward and outward into "tails." It is not clear what effect such prolongation of the wings may have upon the flight of the insects, but it is

Fig. 29.—*Actias maenas*, an Indian Moth of the family *Saturniidae*. The hind wings are prolonged backward into long balancers (see 115).

interesting to note that the same form of "tail" has been independently evolved in Moths and Butterflies.

In some Lepidoptera of the family Saturniidae (e.g. *Actias*, fig. 29, *Eudaemonia* and *Copiopteryx*), and of the families Zygaenidae (e.g. *Himantopterus*), Lycaenidae and Hesperidae, the hind wings are drawn out into long thread-like or lamellar balancers with roughly spiral or wrinkled leaf-like ends, almost exactly like the hind wings of the Nemopterous Neuroptera (e.g. *Halter* and *Kirbynia*, fig. 33). These balancers do not participate in the flapping of the wings, but trail behind in a passive manner.

An explanation that has been offered is that the "tails" have a protective value and enable the Moth to escape from a predatory Bird with the loss of the ends only. This is perhaps supported by the presence in some Moths of an enlarged extremity to the "tail" with a special mark, the "directing mark."

A

B

Fig. 30.—A, a rapidly flying Moth (*Pseudosphinx tetrio*), and B, a slowly flying Moth (*Saturnia pavonia-major*), showing the differences in the shapes of the wings and in their superficial area (see 119–120).

117–118. Owl Moth, *Noctua strix*, South America, and Atlas Moth, *Attacus atlas*, India. These species of Moths are among the largest Lepidopterous Insects known; they attain a greater size than the specimens here shown. Such Moths are not,

however, by any means the largest flying insects on record, for some of the extinct Dragon-flies of the Carboniferous Period measured two feet across the wings. See outline sketch of *Meganeura monyi*, 127, on the back of Case 3.

119–121. A rapidly flying Moth, *Pseudosphinx tetrio*, and a slowly flying Moth, *Saturnia pavonia-major* (fig. 30, A and B). Also a Burnet Moth, *Zygaena filipendulae*. Among the Lepidoptera the most rapid and powerful fliers have longer and narrower wings, with a straighter front edge, than the more leisurely and feeble fliers. They not only move through the air at a higher speed, but the rate of flapping of the wings is also greater than in the case of more slowly travelling Butterflies and Moths. The Burnet Moths might in a way be regarded as exceptions, for they fly about lazily and yet have rather long, narrow front wings.

122. Left front and hind wings of a male Hawk-Moth, *Pseudosphinx tetrio*, seen from below, showing the frenulum and

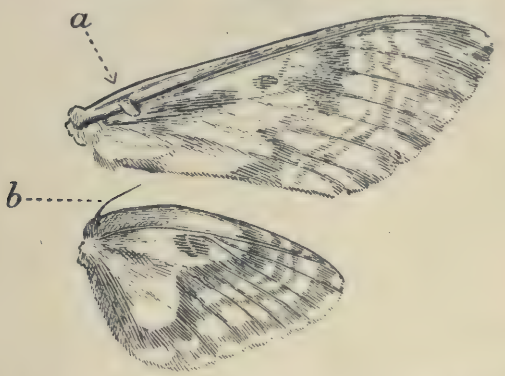

Fig. 31.—Left front and hind wings of a Death's-head Moth (*Acherontia atropos*), seen from below, showing the retinaculum (*a*) and the frenulum (*b*) (see 122).

retinaculum. In Lepidoptera the front wing overlaps the hind wing, so that in flight the two wings of the same side must act in co-ordination. In most Moths, but not in Butterflies, this co-ordination is secured by a frenulum, which projects from the front edge (costa) of the hind wing, and is secured into a retinaculum situated on the under side of the front wing, near the base. In the large majority of Moths the retinaculum descends

from the costal nervure in the male, while in the female it ascends from the median nervure. In the female the frenulum consists in most cases of three separate bristles, but in the male it is a composite structure usually in the form of a single curved bristle. See microscope slides D and E, and fig. 31. In the Orders of Insects other than the Lepidoptera the hind wing is secured to the front wing of the same side of the body by other means; see the labels referring to the Hymenoptera and Hemiptera.

123. Left front and hind wings of a Ghost-Moth, *Hepialus humuli*, after removal of the scales, showing the jugum. In a few Moths (the Hepialidae, or Ghost-Moths, and the Micropterygidae) there is no frenulum, but a small lobe, the jugum, projects from the base of the hind edge of the front wing towards the hind wing, and may serve to secure a feeble connection between the two wings of the same side.

Dragon-flies, etc. (Neuroptera).

In most Neuropterous Insects both front and hind wings are used for flight; they are clear and transparent and have a net-like venation. They are approximately equal in size in Dragon-flies, Ant-lions and Lace-wings (fig. 32), but in the May-flies (fig. 32) the hind wings are small. In the Nemopteridae (e.g. *Kirbynia* and *Halter*, fig. 33) the second pair of wings are in the form of long balancers. The Neuroptera include some of the largest Insects known (see 127).

124. An American Dragon-fly, *Megistogaster lucretia.* The front and hind wings are of the same size.

125. *Kirbynia sheppardi* (fig. 33), a Neuropterous Insect of the family Nemopteridae. The hind wings are in the form of long balancers. In some Nemopteridae, e.g. *Halter imperatrix*, the balancers are longer and more slender (fig. 33, lower figure).

126. May-fly, *Ephemera vulgata* (fig. 32). The hind wings are much smaller than the front wings.

127. (In frame on the back of Case 3). Outline sketch, of the natural size, of *Meganeura monyi*, one of the giant Dragon-flies of the Coal Measures of Commentry, France. The span of the wings measures a little over two feet. (Figure copied from C. Brongniart, "Insectes fossiles des temps primaires," 1893, Atlas, Plate 43.)

Fig. 32.—Neuropterous Insects—Lace-wing (*Chrysopa perla*) and May-fly (*Ephemera vulgata*). In the Lace-wing (upper figure) the hind wings are only slightly smaller than the front wings; in the May-fly (lower figure) they are considerably smaller (see 126).

Fig. 33.—Neuropterous Insects of the family Nemopteridae—*Kirbynia sheppardi* (upper figure) and *Halter imperatrix* (lower figure). The hind wings are modified into balancers, and do not beat the air during flight (see 125).

Wasps, Bees, Ants, etc. (Hymenoptera).

In Hymenopterous Insects the wings are four in number; they are membranous, and usually transparent. Both front and hind pairs are used for flight (except in wingless worker Ants, etc.),

and the hind pair are smaller than the front pair. In Wasps and Bees the two wings of the same side move as one structure owing to a series of small upwardly directed hooks on the front margin of the hind wing fitting over a downwardly projecting ledge on the hind margin of the front wing. See slide A shown under the microscope, and fig. 41.

128–130. A Hornet, *Vespa crabro*, an Ichneumon, *Ephialtes manifestator*, and a Saw-fly, *Sirex gigas*, as examples of Hymenopterous Insects.

Beetles (Coleoptera).

In Coleopterous Insects the second pair of wings alone are organs of flight, the first pair being modified into hard, shell-like structures (elytra), beneath which the functional wings can be folded up. In some Beetles (*e.g.* Stag-Beetle and *Macrotoma*) the elytra are lifted up during flight, and in consequence of their concavo-convex shape they may be of some value in maintaining the body in the air. In other Beetles the elytra are during flight only raised sufficiently to allow of the emergence of the wings below their outer edges (*e.g.* Goliath-Beetle, Rose-Beetle).

131–132. Examples of Beetles which raise the elytra during flight—Stag-Beetle, *Lucanus cervus*, Europe, and *Macrotoma coelaspis*, Tropical and South Africa.

133–134. Examples of Beetles which during flight raise the elytra only sufficiently for the emergence of the wings—Goliath-Beetle, *Goliathus giganteus*, Tropical Africa, and a Chinese Rose-Beetle, *Protaetia speculifer*.

Flies (Diptera).

Dipterous Insects, or Flies, have only the first pair of wings developed as organs of flight (fig. 34); the second pair are reduced to small stalked balancers or "halteres" (fig. 43). For the structure and relations of these last see the enlarged models of House-Fly, Tsetse-Fly and Mosquito in the middle of the Hall.

The halteres are characteristic of the Diptera, though they are absent in most of the wingless forms of the order. The halter in most cases resembles a pin, being a slender rod with an

enlarged rounded head, but the form of the head varies considerably. The function of the halteres is not clear; the most probable assumption is that they act as sense organs. Each is provided at its base with muscles, and can, like the wings, execute rapid vibrations. Since the halteres are the homologues of wings, it is remarkable that in none of the Diptera are they represented by wings or by structures intermediate in character between balancers and wings.

Fig. 34.—A Horse-Fly (*Tabanus bovinus*). Nat. size.

135–137. An African Horse-Fly, *Tabanus ruficrus;* a British Mosquito or Gnat, *Theobaldia fumipennis;* and a large South American Fly, *Pantophthalmus championi;* as examples of Dipterous Insects.

LOCUSTS, COCKROACHES, ETC. (ORTHOPTERA).

In most of the Orthoptera (*e.g.* Locust, fig. 35) the front pair of wings (tegmina) are stiffer than the second pair, and protect the latter when the insect is not flying.

Fig. 35.—A common migratory Locust (*Schistocerca tartarica* = *Acridium peregrinum*). Three-fourths (linear) of the natural size.

138. An African Locust, *Cyrtacanthacris lineata*, as an example of an Orthopterous Insect.

Bugs, Cicadas and Aphids (Hemiptera or Rhynchota).

In Hemipterous Insects both pairs of wings are usually developed. In one division (Heteroptera) the front wings are firmer and darker than the hind wings, but this is not the case in the Homoptera (*e.g.*, Cicadas and Lantern-flies). In many cases the hind wing is secured to the front wing in such a manner that the two wings of the same side move as one structure. In Water-Bugs there is a single hook near the back of the front wing which fits into an upwardly directed flange on the front edge of the hind wing. In Cicadas and Lantern-flies the hind margin of the front wing is turned down for a part of its length, and hooks over an upturned portion of the front margin of the hind wing. See slides B and C shown under the microscope.

139–141. A Trinidad Water-Bug, *Belostoma grandis ;* a Bornean Cicada, *Pomponia imperatoria ;* and a Lantern-fly, *Fulgora candelaria ;* as examples of Hemipterous Insects.

142. Diagram of a section taken through the wings of a Cicada or a Lantern-fly showing the mode of interlocking. See fig. 36.

Fig. 36.—Diagram of a section taken through the wings of a Cicada, or a Lantern-fly, showing the mode of interlocking.

FOLDING OF THE WINGS OF INSECTS.

The specimens that follow illustrate the mode of disposal of the wings of Insects on their coming to rest. The term "folding" is in this connection commonly used in two different senses, (*a*) the disposition of the wings with regard to the body, and (*b*) the bending or doubling up of the individual wings. Thus it is customary to speak of the wings being folded up vertically over the back in Butterflies and Dragon-flies, and folded like a gable-roof over the abdomen in Moths and Ant-lions. Here there is no

wrinkling or doubling up of the individual wings such as occurs in the hind wings of Earwigs and Beetles.

Lepidoptera.

Most Butterflies (143) on coming to rest set the wings straight up over the body, the upper surfaces of the front wings being almost in contact. Most Moths (144) in a state of rest dispose their wings backward over the abdomen, the front wings covering the hind wings, and presenting the form of a gable-roof. Some Moths, however, such as most of the Geometer-Moths (145), rest with the wings widely spread, almost as in flight. Some of the Plume-Moths (146) fold up the two wings of the same side in a line at right angles to the body, so that the wings and the body present more or less the appearance of the letter T; but the Many-plume Moth (*Orneodes*) settles with wings expanded, presenting the characteristic appearance which has earned for it the name of Fan-Moth. Other Moths, such as the Lappet-Moths, Poplar Hawk-Moth (147), Lime Hawk-Moth, etc., rest with the wings spread sideways, the front wings sloping backward over the hind wings.

143. A Butterfly (Camberwell Beauty, *Vanessa antiopa*) in the attitudes of flight and rest. In a state of rest the wings are set vertically above the body.

144. A Moth (Indian Death's-head Moth, *Acherontia atropos styx*) in the attitudes of flight and rest. In a state of rest the wings slope backwards over the abdomen, the front wings covering the hind wings and presenting the form of a gable-roof.

145. Small Dusky Wave-Moth, *Acidalia virgularia*, one of the Geometer-Moths, in a state of rest—an example of a Moth which rests with the wings widely spread, almost as in flight.

146. A Plume-Moth, *Pterophorus monodactylus*, in the attitudes of flight and rest. The two wings of the same side close up in a line at right angles to the body, the wings and the body thus presenting the appearance of the letter T.

147. Poplar Hawk-Moth, *Smerinthus populi*. In a state of rest the hind wings remain as much outspread as in flight; the front wings slope backward over them.

Neuroptera.

In Neuropterous Insects the two pairs of wings may in a state of rest be held vertically over the back, as in Dragon-flies (148), or may fold over the abdomen in the form of a gable-roof, as in Ant-lions (149), or over the abdomen horizontally, as in the Perlidae (150), only one of the front wings being then visible. The individual wings usually remain flat, but in the Perlidae the hinder portions of the second wings become plicate.

148. A Dragon-fly, *Pantala flavescens*, in the attitudes of flight and rest.

149. An Ant-lion, *Palpares speciosus*, in the attitudes of flight and rest.

150. A Perlid, *Perla* sp., in the attitudes of flight and rest.

Hymenoptera.

In the Wasps (true Wasps, Diploptera or Vespidae, *e.g.* Hornet, 152) the wings are sloped straight backward when the insect comes

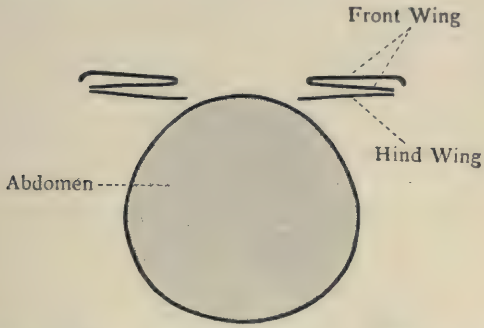

Fig. 37.—Section across the abdominal region of a Hornet (*Vespa crabro*), showing the shape of a Z presented by the cut edges of the doubled front wing and the hind wing underneath it.

to rest, and the front wings undergo a longitudinal folding in such a manner that each appears V-shaped in cross section. The hind half of the front wing folds under the front half, and so there is no necessity for the unhooking * of the fore and hind wings of the same side. In all other Hymenoptera—Sand-Wasps, Bees

* The mode of hooking of the hind wing upon the fore wing in Hymenoptera is illustrated by slide A shown under the microscope.

(*e.g.* 151), Saw-flies, etc.—excepting of course the wingless forms, the wings remain flat when in a state of rest.

151. Humble-Bee or Bumble-Bee, *Bombus terrestris*, in the attitudes of flight and rest.

152. Hornet, *Vespa crabro*, in the attitudes of flight and rest.

153. Diagram of a section across the abdominal region of a Hornet, *Vespa crabro*, showing the shape of a Z presented by the cut edges of the doubled front wing and the hind wing underneath it (see fig. 37).

Orthoptera.

In most Orthoptera the front wings are stiff and are known as tegmina. Like the elytra of Beetles, they close over the hind wings and protect them when the insect is at rest. The hind wings in Locusts (155, fig. 35) and Grasshoppers are large, and fold up in a fan-like manner beneath the tegmina. In the Fan-wing (156, fig. 38) the resemblance to a fan is even greater than in the Locusts; the front edge of the wing is stiff, and the tegmina are short and narrow. In the Cockroach (154) it is only the hinder part of the wing which folds up in a fan-like manner.

154–156. A Cockroach, *Periplaneta americana*, a Locust, *Orthacanthacris aegyptia*, and a Fan-wing, *Rhipipteryx limbata*, showing the differing degrees to which the hind wings are capable of folding up in a fan-like manner.

Fig. 38.—Fan-wing (*Rhipipteryx limbata*). (× 3). The hind wings are large, and fold in a fan-like manner (see 156).

157. Earwig (*Forficula auricularia*, fig. 39). The first pair of wings, or tegmina, are stiff and are not used for flight; they serve to protect the second pair or wings proper when these are not in use. The mode of folding up of the wings is highly complicated, and is here explained by the paper models A–F, enlarged seventeen times linear. The drawing A shows the shape of the wing (right wing, seen from above), the arrangement of the veins of the wing (in black), and the lines of folding (in red). The black and red lines are not repeated in the models B–F. When the wing of the Earwig folds up on the insect coming to rest after flight, the whole of it except the basal part folds after the manner of a fan (B). When the fan is nearly closed, it bends sharply in

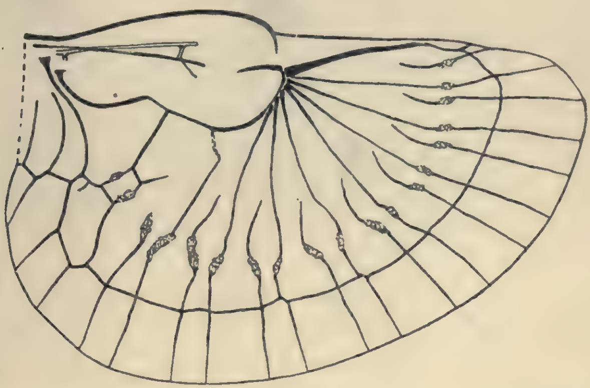

Fig. 39.—Wing of an Earwig (*Forficula auricularia*). (× 8.) (See 157.)

the middle of its length (C and D) and comes to lie compactly under one half of the basal part of the wing (E). This half of the base of the wing then folds under the other half (F), and the process is complete.

On the card at the right lower corner of the series are shown four actual specimens of right wings in phases of unfolding.

Diptera.

In Dipterous Insects or Flies the wings remain flat in a state of rest. They are sloped somewhat backward, as in Blow-Flies (158) and House-Flies, or may be so much directed backward that the one wing completely covers the other, as in Tsetse-Flies (159).

158–159. A Blow-Fly, *Calliphora erythrocephala*, and a Tsetse-Fly, *Glossina palpalis*, in the attitudes of flight and rest.

COLEOPTERA.

In Coleopterous Insects or Beetles the front wings are modified into hard, shell-like elytra, which do not beat the air during flight, but which serve to protect the hind wings, or wings proper, when the insect is at rest. The wings are much larger than the elytra, and in order that they may be stowed away beneath the wing-covers they are provided with special means of folding up.

160. Goliath-Beetle, *Goliathus giganteus*, dissected to show the mode of folding of the wings when at rest. The elytra have been removed so as to expose the wings; the right wing is shown fully folded, the left wing partially folded. Below the Beetle is the left wing, fully extended, from another specimen (see fig. 40).

In the three wings shown, *a* marks the part which is hinged upon the body; *b* is the folding joint, the place where the outer half of the wing folds upon the basal half, somewhat after the manner of the blade of a pocket-knife; *c* is the tip of the wing, which when the insect is at rest is set close to the basal part of the wing of the opposite side.

161. Goliath-Beetle, *Goliathus giganteus*, in the attitude of rest. The wings are completely concealed beneath the elytra.

162. A curious Carabid Beetle, *Mormolyce phyllodes*, from the Malay Peninsula, in the attitudes of flight and rest. The edges of the elytra are produced into flat leaf-like expansions, so that the elytra as a whole are larger than the wings. The wings fold up beneath the middle part of the elytra, not under the lateral plates. Very possibly these plates act as "planes," serving to maintain the weight of the body in the air, while the wings supply the motive power to drive the body forward through the air.

163. *Ctenoscelis acanthopus*, a Longicorn Beetle of the sub-family Prioninae. Whereas in the Goliath-Beetle (160, fig. 40) the joint in the wing (*b*) occurs about half-way between the hinge (*a*) and the tip (*c*), in this and most Longicorn Beetles the joint occurs much nearer to the tip than to the hinge. In the specimen shown the elytra are removed, and the left wing is expanded as in flight, while the right wing is folded.

In certain genera of the family Cerambycidae, the joint in the wing is rather near the tip, and the elytra being relatively small,

the wings are freely visible when the insect is at rest. In the genera *Necydalis* and *Clytarlus* the position of the joint near the

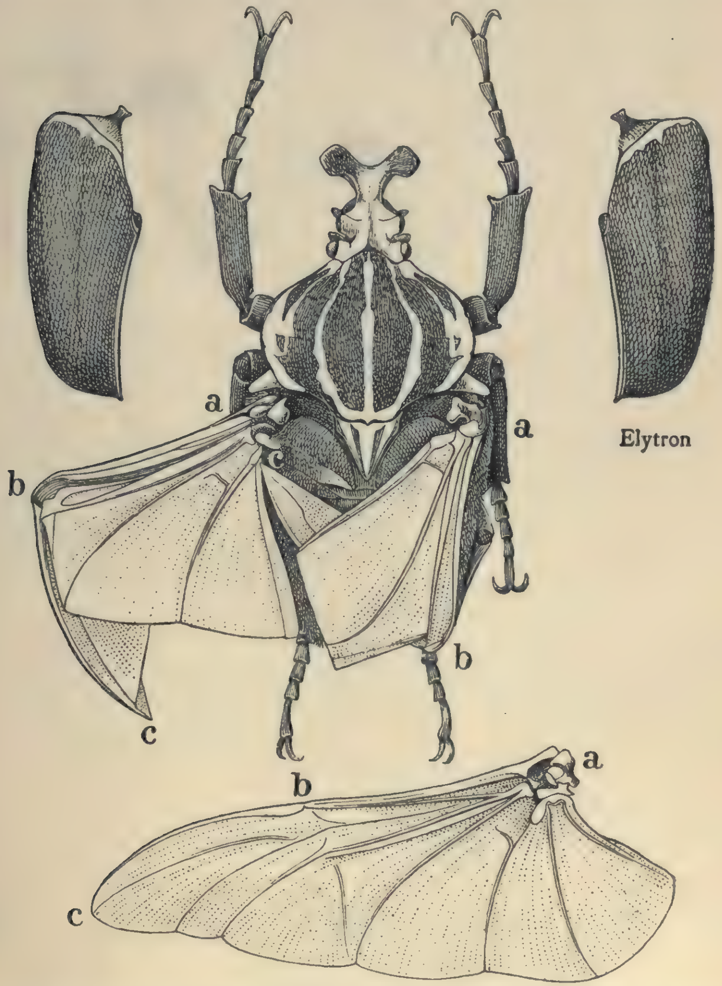

Fig. 40.—Goliath-Beetle (*Goliathus giganteus*), dissected to show the mode of folding of the wings when at rest. (For explanation see 160.)

end of the wing is recognisable, but the joint is functionless, and the wings remain flat when not in use—such insects do not look like Beetles, and are mostly mimetic forms.

164. Cock-tail or Devil's Coach-horse Beetle, *Ocypus olens*, with the right elytron removed to show the much folded wing. On the card are mounted the wings of three other specimens, together with the pair of elytra of one of them. The upper pair of wings are fully expanded; *a* marks the base or hinge, *b* the principal joint, situated nearer the base than in the Goliath-Beetle (160), and *c* the tip of the wing. The pair of wings mounted below these show the first stage in the process of folding, the part *b c* becoming bent at right angles to the part *a b*. The next pair exhibit a folding of the part *b c* along the lines indicated by the vertical pencil marks, dividing the right wing into three parts and the left wing into two. The tips of both wings thus come to point to the left. The two wings when fully closed are completely concealed beneath the two elytra. In some individuals it is in the left wing that the part *b c* folds into three, and in the right wing into two.

Hemiptera or Rhynchota.

In the Homopterous division of the Hemiptera (*e.g.* Cicadas, 165) the four wings usually fold over the abdomen at an angle, presenting the form of a gable-roof, when the insect comes to rest; in the Heteropterous division the wings usually fold flat upon the abdomen (*e.g.* Water-Bugs, 166).

165–166. An Australian Cicada, *Henicopsaltria eydouxii*, and an Indian Water-Bug, *Belostoma indica*, in the attitudes of flight and rest.

CASE 4.

MICROSCOPE SLIDES ILLUSTRATING CERTAIN FEATURES OF THE WINGS OF INSECTS AND FEATHERS OF BIRDS.

Slide A—Middle part of the left fore and hind wings of a Humble-Bee, *Bombus lucorum;* under surface. The two wings are separated, but in the living insect the hooks seen along the edge of the hind wing hook upon the scroll-like edge of the front

wing, so that during flight the two wings move as one structure (see fig. 41).

Slide B—Middle part of the right front wing of an Arabian Water-Bug, *Laccotrephes fabricii;* under surface. The short,

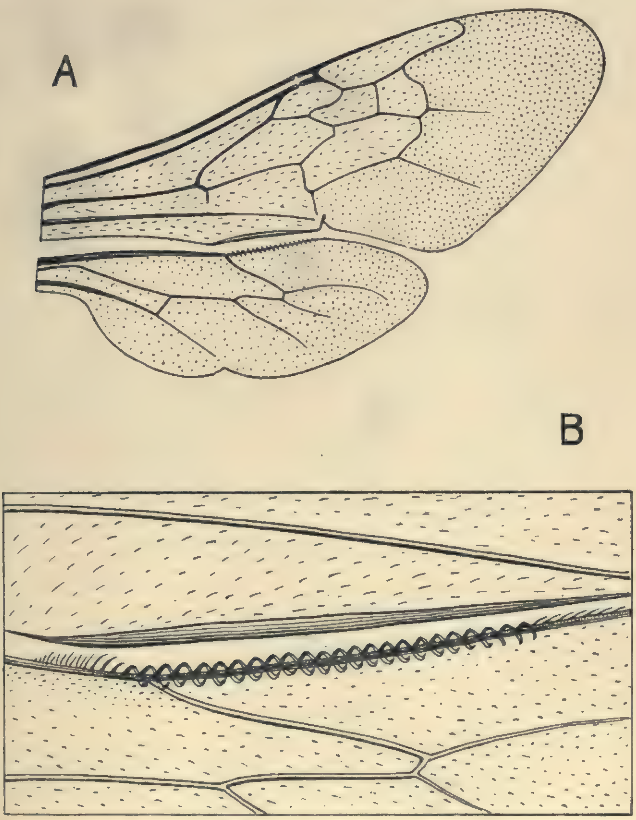

Fig. 41.—Wings of a Humble-Bee (*Bombus lucorum*). A, front and hind wings of the left side seen from below. The hind wing is in the living animal securely fastened by the row of hooks along the middle part of its front edge to the curved scroll that occurs in the middle part of the hind edge of the front wing, but in this figure the wings are drawn separated, so as to show more distinctly the hooks of the scroll. B, the middle part of figure A further enlarged, showing the row of hooks along the front edge of the hind wing and the scroll along the hind edge of the front wing (see microscope slide A).

broad hook, brown in colour, which is seen standing out towards the observer, fastens over a scroll-like front margin of the

hind wing, so that during flight the two wings move as one structure.

Slide C—Middle part of the left hind wing of a South European Cicada, *Tettigia orni;* upper surface. The upturned scroll of the front edge of the hind wing hooks beneath the scroll-like hind edge of the front wing, so that during flight the two wings move as one structure (see fig 36).

Slide D—Basal portions of the left front and hind wings of the male of a small species of Hawk-Moth, *Macroglossa trochiloides;* under surface. The scales have been removed. A long, curved, tapering bristle, the frenulum, projects from the front edge of the base of the hind wing, and fits into a kind of recurved strap or hook, the retinaculum, on the under side of the front wing (see fig. 31). This mode of ensuring a co-ordinated action of the two wings of the same side of the body is common among Moths, but does not occur in Butterflies (see 122).

Slide E—Isolated frenula of the female and male of a Tineid Moth, *Cryptophaga epadelpha.* In this, as in most Moths, the frenulum of the female consists of a few (usually three) bristles, and that of the male of a single structure, longer and thicker than the bristles of the female.

Slide F—A piece of the front wing of a Death's-head Hawk-Moth, *Acherontia atropos;* upper surface. The scales are ordinary scales such as are characteristic of Moths and Butterflies, which insects are denoted Lepidoptera because of their scaly investment (Greek; *lepis* (*lepid-*), a scale; and *pterón*, a wing).

Slide G—A piece of the front wing of a South African Emperor-Moth, *Gynanisa maia;* under surface. The region selected shows a transition from ordinary scales such as are seen in slide F to very long scales (see fig. 42, A, D, E). The elongation is shared by the teeth of the scales as well as the bodies of the scales. The parts of wings bearing such scales have the appearance of a soft fur.

Slide H—A piece of the front wing of a Convolvulus Hawk-Moth, *Protoparce convolvuli*, taken from near the hind edge; upper surface. The region selected shows a transition from ordinary scales to very long scales in which the teeth are not longer than in ordinary scales (see fig. 42, A, B, C). The parts

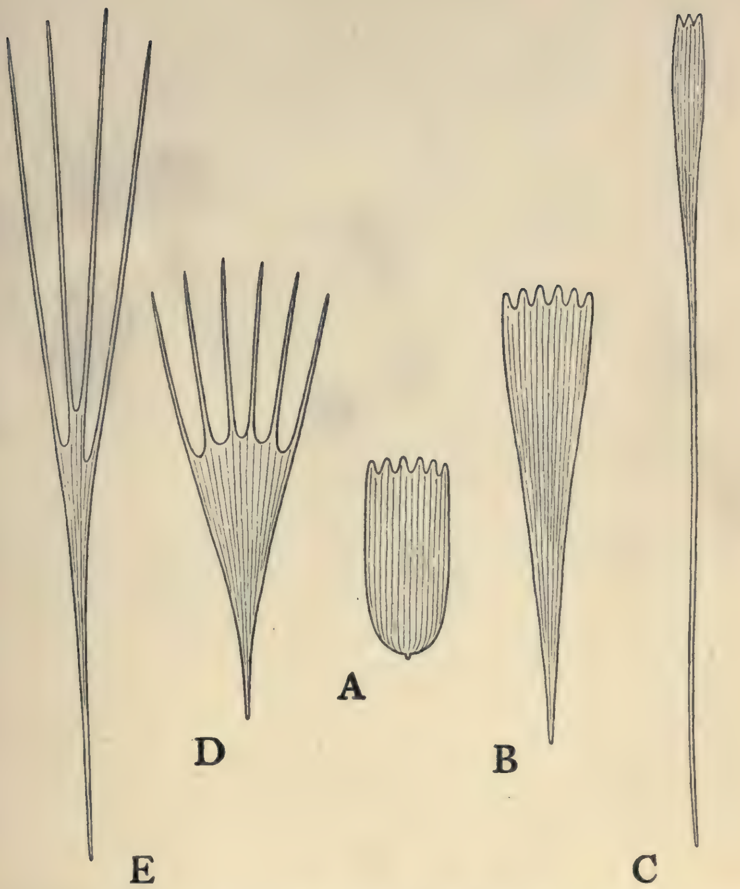

Fig. 42.—Diagrams of Scales of Moths, greatly enlarged. A, a typical scale such as is found on the wings of most Lepidoptera. The scale is attached by a short narrow stalk, and the free edge is provided with a number of projections or teeth. B, a long narrow scale, and C, a very long scale, almost like a bristle, with a small flattened part near the free end, and with a few teeth only. D, a scale with elongated teeth, and E, a long scale with very long teeth, fewer in number than those of scales such as A and D. The hairy or furry patches on the wings of Butterflies and Moths owe their peculiar appearance to scales such as those of type C or those of type E. Both kinds of elongated scales (C and E) may occur together. Figures A, B and C are drawn from scales of the wing of the Light Crimson Underwing Moth (*Catocala promissa*), and figures D and E from those of a South African Emperor-Moth (*Gynanisa maia*) (see microscope slides F, G, and H).

of wings bearing such scales have the appearance of a coarse or bristly fur.

Slide J—Left wing of a House-Fly, *Musca domestica ;* upper surface. In Flies (Diptera) only the first pair of wings are developed as organs of flight, the second pair being modified into small stalked balancers or "halteres." In slide J the halter is seen through the hood-like extension of the base of the wing,

Fig. 43.—Left wing of a House-Fly (*Musca domestica*), with the halter (*h*) showing through the transparent squama (*s*) (see microscope slide J).

known as the "squama" (see fig. 43). The halter is, so far as can be judged, a sense organ enabling the animal to maintain the equilibrium of the body.

Slide K—*Caraphractus cinctus*, a minute Hymenopterous insect of the family Mymaridae (see fig. 44). The special interest attaching to this insect is that it flies under water, or swims by means of its wings (compare the Penguins among Birds). The Mymaridae are commonly known as Fairy-flies, and include some of the smallest winged insects known. *Caraphractus cinctus* is aquatic in habit, and lays its eggs in the eggs of Dragon-flies.

Slide L—Portion of a wing-feather of the Bearded Vulture, *Gypaetus barbatus*, upper surface, showing the manner in which the barbules of the one side of each barb fasten by means of their hooklets upon the scroll-like edges of the barbules of the other side of the next barb, across which they lie obliquely (see fig. 20, B and C). In the slide two of the barbs have been partly separated from the rest so as to show more distinctly the form of the barbules. For further details of the structure of a feather see the enlarged model 63 B.

Slide M—Portion of a feather of the American Ostrich, *Rhea americana.* The barbules on the two sides of each barb are alike; they have neither scroll-like edges nor hooks such as are seen in

Fig. 44.—*Caraphractus cinctus*, a minute aquatic Hymenopterous insect which flies under water, or swims by means of its wings. The hind wings are reduced in width, and both front and hind wings are fringed with hairs (see slide K).

the feather of the Vulture (slide L). Feathers of this type are more fluffy than those in which the barbules are hooked together. Compare fig. 20, A, with fig. 20, B and C.

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